Tortrix australis Gray, 1841, a senior synonym of *Demansia reticulata* (Gray, 1842) (Elapidae)

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ABSTRACT – The long-forgotten snake name *Tortrix australis* Gray, 1841 is shown to be a senior synonym of *Demansia reticulata* (Gray, 1842), an elapid species from Western Australia. The holotype, originally lodged in the collection of the Museum of the Army Medical Service at Chatham, now lost, is likely to have been collected from the Perth area, through the auspices of one of the surgeons associated with army regiments assigned to Australia. The most likely source of the specimen is Dr William Milligan, who was stationed in the Swan River Colony between 1830 and 1834. Through designation of a neotype and use of Article 23.9 of the Code of Zoological Nomenclature, *Demansia reticulata* is made a nomen protectum, and *Tortrix australis* a nomen oblitum, stabilising nomenclature.

KEYWORDS: *Demansia*, Elapidae, nomenclature, synonymy, Chatham Museum, William Milligan

INTRODUCTION

In a recent paper, Nankivell et al. (2023) provided resolution of the *Demansia psammophis* species complex (Elapidae), recognising three species: *D. psammophis* (Schlegel, 1837) in eastern Australia, *D. reticulata* (Gray, 1842) in the western parts of Western Australia, and a new species in intervening areas, *D. cyanochasma*. The only previous formal taxonomic treatment of these, by Storr (1978) and covering only the Western Australian members of the complex, had recognised a more widespread *D. reticulata*, with a northern/inland subspecies *D. reticulata cupreiceps* Storr. However, Storr et al. (1986), with additional material having accumulated in the Western Australian Museum collection, partially recanted Storr's previous conclusions, suggesting that both were subspecies of *D. psammophis*, and that his *D. reticulata cupreiceps* was divisible into two entities, one of which represented a western population of *D. psammophis psammophis*. The informal nature of this rearrangement, included in a field guide without any analysis, and without consideration of variation within eastern Australian populations of *Demansia psammophis*, led to uncertainty over the taxonomy of the complex, with a variety of nomenclatural combinations appearing in the literature over the following 40 years: *D. psammophis*, *D. p. psammophis*, *D. reticulata*, *D. r. reticulata*, *D. p. reticulata*, *D. r. cupreiceps* and *D. p. cupreiceps*. Uncertainty over the location of potential contact zones between the three entities led to many authors simply using an expanded *D. psammophis* as the name for all of these. Hutchinson and Tyler (1996) recognised a parapatric distribution of two taxa in the Flinders Ranges, using the name *cupreiceps* for the taxon in the lowlands to the west of the ranges, and *psammophis* for the species in the ranges, and to the east. Further complicating the nomenclature was the purported type locality of *D. psammophis* being from King George Sound in Western Australia (Duméril et al. 1854), outside the range of any *Demansia* species, but closest to *D. reticulata*. The work by Nankivell et al. (2023), using larger samples than available to Storr 45 years earlier, and with sequence data, provided further validation of the parapatric distribution of two entities in South Australia, identified only two taxa in Western Australia, and recognised all three as full species. However, their work changed the position of the boundary between the south-western species and the inland species. As a result of the type locality of *D. reticulata cupreiceps* now being within the range of *D. reticulata*, the inland species was described as a new taxon.

Nankivell et al. (2023) considered the type material of *Elaps psammophis* Schlegel, 1837, and *Lycodon reticulatus* Gray, 1842, identifying the former as representing the eastern Australian taxon, and the latter as representing the western taxon. However, they did not note the existence of a name that antedates *D. reticulata*, and which potentially imperils that name.

Gray's description of *Lycodon reticulatus* was published in a paper that spanned two issues of his occasional series, The Zoological Miscellany. The first six pages, including the description of *Lycodon reticulatus*, were published in an issue bearing an imprint date of April 1842. The last page, containing descriptions of two frogs, appeared at the beginning of the next issue, with an imprint date of May 1842.

Synonymy of *Tortrix australis* Gray, 1841 with *Demansia reticulata* (Gray, 1842)

In a publication likely written after September 1841, and released about November 1841 (Shea et al. 2020), just five months before he named *Lycodon reticulatus*, John Edward Gray (1841) compiled a listing of the reptiles of Australia as an appendix to the published journals of the explorer George Grey. This account included a short description of a new species, *Tortrix australis*. The name appears twice. On p. 432, there is only a brief mention:

> '74. *Tortrix australis* — Gray.
>
> Inhab. New Holland, Mus. Chatham, n. 68.'

This was followed by a description on p. 444:

> '74. *Tortrix australis* — Pale olive, scales black-edged, on the sides widest; beneath bluish, with a white edged black band across the end of the muzzle; a white band before the front and back of the eyes, and a triangular black spot at the lower hinder angle of the eyes; pupil round; one large and two posterior ocular shields, no loreal shields; nostrils lateral, in the suture between the two nasal shields; scales smooth imbricate, those of the sides larger, of the tail six-sided.'

The name was not mentioned in subsequent literature, including the two later catalogues of snakes by Gray's successors at the British Museum (Günther 1858; Boulenger 1898). The only subsequent mentions I can locate of *Tortrix australis* are by Cogger et al. (1983), who list it as a species inquirenda, and Wallach et al. (2014), who follow Cogger et al. (1983) in so listing it.

While neither of the mentions of the name by Gray (1841) explicitly gives a locality for his species, it was published in a paper that was a list of the reptiles of Australia, and the title states that the new species were from Western Australia, although only a few of them are specifically listed as from there. With the redefinitions and redescriptions of the species of *Demansia* provided by Shea (1998), revising the northern Black Whip Snakes, Shea and Scanlon (2007), revising the smaller tropical species of Whip Snakes and Nankivell et al. (2023) revising the southern species, it is possible to unequivocally identify Gray's species as a *Demansia*, due to the facial markings described, and to allocate the name to a species. The trans-rostral dark line, bordered with white, and the pale zones anterior and posterior to the eye, along with the triangular dark patch at the posteroventral angle of the eyes (a teardrop mark), are all characteristics of several *Demansia* species, and in combination are unique to *Demansia* within the Australian snake fauna. Further, the pale olive ground colour of the body with dark-edged scales only fits *D. reticulata* among the *Demansia* species (Nankivell et al. 2023). All of these features are visible on the individual photographed as Figure 1. However, there are two features of *Tortrix australis* that do not fully fit with *D. reticulata*. The first of these is the 'bluish' ventral colour, with *D. reticulata* generally described as having a whitish to yellowish or pale green-white venter (Storr 1978; Storr et al. 1986; Nankivell et al. 2023). A bluish-grey discolouration is a common feature of preservation, and it is possible that the colour is an artefact of preservation of Gray's specimen. Gray also describes the dark teardrop marking under the eye as a triangular black spot, while the teardrop in *D. reticulata* is relatively long, with the tail extending from the subocular supralabial across the length of the fifth supralabial to the anterior part of the sixth supralabial (Nankivell et al. 2023). However, in the absence of details, it is not possible to be sure that Gray's 'spot' was not a 'streak'.

The type of *Tortrix australis* is no longer extant to verify the details of Gray's description. The 'Mus. Chatham' was the Museum of the Army Medical Service at Fort Pitt, Chatham, a natural history collection that was used for training army surgeons and physicians for deployment by the army to various parts of the British Empire, and was supplied with specimens by those medical staff from their various stations. The collection was discarded/dispersed in the 1850s, and specimens are no longer able to be traced. Two catalogues of the natural history collections of the Museum Chatham were published. The first, on birds and mammals, was compiled while the collection was actively growing, and was under the supervision of Edward Burton (Burton 1838). The second, covering reptiles and amphibians, was produced anonymously (Anonymous 1843), but was possibly compiled by the zoologist and physician Andrew Smith, who took over responsibility for the collection from 15 September, 1837 on Burton's retirement (Anonymous 1837), and remained in direct charge of the collection until at least 1841, when he was promoted to Principal Medical Officer at Fort Pitt, becoming responsible for all training and assignment of new recruits to the Army Medical Service (Kirby 1965). By 1845, Smith had left Chatham, being promoted to Professional Assistant in the Office of the Army Medical Department, assisting the Director-General in London (Kirby 1965). Smith, who published extensively on herpetological topics, is attributed as the author on 21 of the names in the catalogue, most of which would remain nomina nuda (three names were

FIGURE 1 Details of colour and pattern of head and body of *Demansia reticulata* from Shay Gap, Western Australia showing the white-edged dark transrostral line, pale lines anterior and posterior to eye, dark teardrop under the eye, and reticulate body pattern on a greenish-yellow ground colour (photo: B. Bush).

validly published at other times: *Cordylus polyzonus* and *C. capensis*, both published by Smith (1838) and *Platydactylus bibronii*, published as *Tarentola bibronii* by Smith (1846)). At the time of publication of the reptile and amphibian catalogue, there is evidence that many of the specimens previously present had already been disposed of. The earliest account of the scope of the collection (Anonymous 1832) reports that 120 reptiles had been donated in that year alone, giving 352 herpetological specimens, of 2718 zoological specimens in total. Burton's catalogue of 1838, four years later, reported the zoological collections to have grown to 9386 specimens. If a similar proportion of herpetological specimens constituted the collection at that date, there would have been of the order of 1200 reptile and amphibian specimens in 1838, and hence presumably more would have been expected to have accumulated by 1843. However, Anonymous (1843) only lists 16 species of chelonians, 4 species of crocodilians, 99 species of lizards, 121 species of snakes and 22 species of amphibians.

Gray (1834, 1838, 1839, 1841) described six species of Australian reptiles from specimens attributed to the Chatham collection: *Lialis burtonis* (Pygopodidae), *Tiliqua stoddartii* (Scincidae, current identification unknown), *Tiliqua vachelli* (Scincidae, current identification unknown), *Lygosoma australis* (= *Hemiergis gracilipes* (Steindachner, 1870), Scincidae), *Tropidonotus mairii* (= *Tropidonophis mairii*, Colubridae) and *Trimeresurus olivaceus* (= *Elapognathus coronatus* (Schlegel, 1837), Elapidae). An additional species, *Elaps lewisii* (= *Dendrelaphis punctulatus* Gray, 1827, Colubridae) was described by Gray (1841) from specimens attributed to Dr Thomas Lewis, a member of the 4th Regiment (and hence likely to also be from the Chatham collection), and the same paper also reported specimens of two Australian snakes already described that were listed as sourced from Dr John Mair of the 39th Regiment, a contributor to the Chatham collection (Shea 2021a).

Of these species, only *Lialis burtonis* (as *L. burtonii*), *Elapognathus coronatus* (as *Elaps coronatus*) and possibly *Demansia reticulata* (*D. psammophis* is listed)

were present in the collection as listed in the 1843 catalogue, all (as with all Australian reptiles listed) with the locality either New South Wales (most species) or New Holland (*Lialis burtonis*, *Morelia spilota* [as *Python peronii*]).

While the herpetological catalogue for the Chatham collection does not list collectors for the specimens, the previous mammal and bird collection does provide lists of the donors to the collections, in order of the number of specimens each person donated. Of those listed for mammals and birds, three are likely to have collected or received specimens from Western Australia, while others are known to have been associated with regiments based in New South Wales (largely around Sydney), and Tasmania. Although based in Sydney, Dr John Mair of the 39th Regiment, after whom Gray named *Tropidonotus mairii*, seems to have received the herpetological specimens collected by Captain Collet Barker, who was commandant of the settlement at Raffles Bay in the Northern Territory, and later at Albany in Western Australia; Barker spent a month in Perth between October and November 1829 between these two assignments, and seems to have collected several snake species there (Shea 2021a). Mair is 23rd on the list of bird donors, but is not listed among mammal donors by Burton (1838). Barker was accompanied during his postings by Dr Robert Martin Davis, assistant surgeon of the 39th Regiment, who is 24th on the list of bird donors (Davis subsequently travelled to Madras with the regiment in 1832, and died there of cholera; Mulvaney and Green 1992). Both Davis and Barker would only have been able to collect *Demansia reticulata* during the month they spent in Perth, as the species does not occur in the Top End of the Northern Territory, or Albany. A much more likely source of a specimen of *Demansia reticulata* is Dr Milligan of the 63rd Regiment, 21st on the list of bird donors presented by Burton (1838).

Milligan is Assistant Surgeon William Milligan, whose life is known in some detail as a result of work by staff at the Perth Hospital, an institution founded by Milligan (Brine and friends 1991). The dates relating to his military career are confirmed by Johnston (1907). Milligan was born at Cavan, Ireland on 1 February 1795, entered the army medical service as a hospital assistant in July 1813, rapidly promoted to Assistant Surgeon in the 82nd Regiment of Foot in February 1814. In January 1819, his first overseas posting was to Mauritius with the same regiment. A year later he returned home, enrolling as a medical student at the University of Edinburgh, graduating in 1822 with a thesis on cholera, a disease he had encountered and studied while in Mauritius. For the next several years, he remained on the half-pay list, apparently also working in private practice in London, and lecturing in Materia Medica and Theory and Practise of Medicine at a London dispensary. On 25 April 1829, Tully Daly, the Assistant Surgeon with the 63rd Regiment, en route to Western Australia with James Stirling, the founding governor of the Swan River Colony, drowned at the Cape of Good Hope when a boat he was in overturned. On 9 July 1829, Milligan was transferred to the 63rd Regiment to fill Daly's place (Anonymous 1829), leaving London with his family aboard the *Wanstead* on 14 August 1829 (Friend 1831), and arriving at the Swan River Colony on 31 January 1830, just months after the colony was founded by Stirling. Milligan remained at the Swan River Colony, with a short period at Albany in January 1834, for four years, until the regiment was posted to Madras. He departed Swan River aboard the *Merope*, on 18 April 1834 (Anonymous 1834). After several years in Madras, Milligan and his family returned to England in 1839, transferred as Surgeon to the 17th Regiment, then to the 76th Regiment in 1840, and finally to the 6th Dragoons in 1844. He retired on 13 February 1847 due to ill health, and died suddenly on 2 September 1851 at his home at 4 Bentinck Terrace, St Johns Wood.

In summary, *Tortrix australis* Gray, 1841 is almost certainly based on the species now known as *Demansia reticulata* (Gray, 1842). If the type locality is Australia, as inferred from the description, the species is certainly a *Demansia*, and best agrees with *D. reticulata*, a Western Australian species. While the type is now lost, the collection that formerly housed it had received zoological specimens, prior to the date of description, from an army surgeon who had been based in Perth (within the range of *D. reticulata*) for four years, or possibly from two other surgeons who had access to material from Perth for shorter periods.

In order to fix the name, given the very slight uncertainty over the synonymy due to possible disagreement in two morphological characters between the description of *Tortrix australis* and the species *D. reticulata*, I designate the lectotype of *Lycodon reticulatus* Gray, 1842, specimen 1946.1.19.79 in the Natural History Museum, London, presented by William Buchanan, as neotype of *Tortrix australis* Gray, 1841. This specimen has been illustrated by Nankivell et al. (2023). This neotype designation fulfils the criteria of Articles 75.3.1–7 of the Code of Zoological Nomenclature.

This permanently fixes *T. australis* as a senior objective synonym of *Lycodon reticulatus*. I further invoke Article 23.9 of the Code of Zoological Nomenclature to make *T. australis* a nomen oblitum, and *L. reticulatus* a nomen protectum, hence maintaining the use of the name *Demansia reticulata* for the species to which it was ascribed by Nankivell et al. (2023) I have been able to locate 32 publications between 1974 and 2023, a period of fifty years, that use the names *D. reticulatus*, *D. reticulatus reticulatus* or *D. reticulatus cupreiceps* (Dell and Chapman 1977, Dell and Harold 1977; Burbidge and George 1978; Storr 1978; Storr and Harold 1978, 1980, 1984, 1985; Storr and Hanlon 1980;

Johnstone 1983; Storr and Johnstone 1983; Storr et al. 1983; Wells and Wellington 1984, 1985; David and Ineich 1999; Ehmann 2005; Shea and Scanlon 2007; Hutchinson 2009; Brandle and Armstrong 2010; Cogger 2014; Wallach et al. 2014; Gambold and Metters 2016; Mirtschin et al. 2017; Shea 2017; Wilson and Swan 2017; Allen and Vogel 2019; Chapple et al. 2019; Eipper and Eipper 2019, 2022; Williams and Maier 2019; Jolly et al. 2023; Nankivell et al. 2023) and an additional 13 publications that use the combination *D. psammophis reticulatus* (Storr et al. 1986; Wilson and Knowles 1988; Gow 1989; Ehmann 1992; Mirtschin and Davis 1992; Golay et al. 1993; Maryan 1996; Aplin and Smith 2001; Bush et al. 2007, 2010; Aplin et al. 2008; Maryan and Reinhold 2009; Gaikhorst 2015), while there have been no publications that use the name *Tortrix australis* as the valid name for the species since 1900. These uses of the name *reticulata* greatly exceed the minimum requirements for Article 23.9.1.2 to be applied (25 works by more than 10 authors over the preceding 50 years, with the interval not less than 10 years).

The question remains as to why John Edward Gray created two different names, in two different genera, based on different type specimens, for what was a single species, all within one year, and why he placed the first species in the genus *Tortrix*, a genus created by Oppel (1811) for three species that are now placed in the genera *Anilius* (Aniliidae) and *Cylindrophis* (Cylindrophidae), very distant from *Demansia* in the Elapidae. While we cannot be sure, it is likely that the answer involves two intersecting principles. Gray was a prodigious worker, and often very slapdash in his approach. Between his first paper on reptiles (Gray 1825), which appeared when he was 25 years old, and his Catalogue of the lizards in the British Museum (Gray 1845), followed four years later by the first part of his Catalogue of the snakes in the British Museum (Gray 1849) — he did not produce the second part, which was left to his successor, Albert Gunther to create (Günther 1858) — Gray wrote vast numbers of papers, not just on reptiles, but also on mammals, birds, molluscs and botany. He emphasised external features in his descriptions, with little interest in internal anatomy as a source of characters, and deliberately made his descriptions brief, as he believed that the purpose of taxonomy was to briefly provide the essential features of taxa to allow rapid discrimination from closely related taxa (Günther 1975). Hence, his often one or two line definitions of higher taxa left much room for errors to be made in assignment. Secondly, in a time before stabilization of principles of binomial nomenclature in zoology, Gray was a prodigious coiner of names, and frequently changed his mind not only on the taxa he recognised, but also on the names he applied to them and what taxa those names would apply to. For example, despite originally creating the scincid genus name *Tiliqua*, he gradually changed the concept of that genus over multiple papers until eventually excluding the species he originally assigned to that name (Shea 2021b). He also paid little attention to the spelling applied to his names, with numerous variants appearing over time.

In the case of *Tortrix australis*, while Gray (1841) did not define the characters of that genus, he did define his concept of *Tortrix* in an earlier paper which presented a broad classification of the Reptilia (Gray 1831). In that classification, Gray recognised three orders within his Section Squamata: Sauri, Ophisauri, and Ophidii, with *Tortrix* in the Ophisauri, along with five other genera. Gray's Ophisauri constituted squamates with 'mouth non dilatable, skin covered with regular equal scales'. Within the Ophisauri, Gray recognised two Sections, Ptygopleura for those squamates with the regular arrangement of scales on dorsal and ventral surfaces separated laterally by a 'compressed line of small scales on each side', containing the genera *Zonurus* (now Cordylidae), *Ophisaurus* (now in Anguidae), *Chalcides* (now divided between Gymnopthalmidae and Scincidae) and *Amphisbaena* (now Amphisbaenidae), and an unnamed Section II for squamates with 'body covered with imbricate scales', containing the genera *Scincus* (now Scincidae), *Bipes* (species spread over Diploglossidae, Pygopodidae and Scincidae), *Anguis* (now Anguidae), *Tortrix*, *Acontias* (now in Scincidae) and *Typhlops* (now Scolecophidia). Amongst these six latter genera, *Tortrix* was defined as 'body long, cylindrical; back covered with imbricate scales; beneath with larger scales; tongue short, contractile, two-cut; head long' — essentially a snake in the modern use of that word. Hence, if a species was considered to belong to his Ophisauri (which would effectively be reduced to a decision on whether the mouth was distensible or not) then any snake with enlarged ventral scales would be allocated to the genus *Tortrix* by default. However, by the time of his later Catalogue of the Snakes in the collection of the British Museum (Gray 1849), he had returned *Tortrix* to being a genus of true snakes, and restricted it to *Anilius scytale* (Linnaeus, 1758). It is likely that between his 1841 and 1842 papers, he had either recognised his error in placing his new species *australis* in *Tortrix*, and wished to avoid any mention of that mistake, so providing a new species name as well, or he had simply forgotten or overlooked the species he described as *Tortrix australis* when describing *Lycodon reticulatus*, as the name *Tortrix australis* was not classified anywhere close to *Lycodon* and so did not need to be compared to the specimens donated by Walter Buchanan to the British Museum that would become the types of *L. reticulatus*.

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A collection of mites in the family Laelapidae from rodents in Western Australia

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ABSTRACT – This paper reports on four species of parasitic mites in the family Laelapidae from rodents in the Shark Bay World Heritage Area of Western Australia. New host and locality information is provided for *Laelaps lybacia* Domrow, 1979, *L. rothschildi* Hirst, 1914, *L. spatanges* Domrow, 1973, and *Mesolaelaps australiensis* (Hirst, 1926). The male of *L. lybacia* is described for the first time.

KEYWORDS: *Laelaps*, *Mesolaelaps*, habitat restoration, Dirk Hartog Island

INTRODUCTION

Dirk Hartog Island is the largest island in Western Australia, and lies in the Shark Bay World Heritage Area (Christensen and Jones 2020). It is the subject of a habitat restoration project following the eradication of sheep, cats and goats. As part of that project, native rodents are being re-introduced to the island (Algar et al. 2020; Cowen et al. 2021; Sims et al. 2021). Ectoparasites collected from rodents during that process and during the associated ecological monitoring contribute useful new information about the geographic distribution of and host range of four species of mites in the family Laelapidae Canestrini, 1891.

MATERIALS AND METHODS

Rodents were trapped as part of the translocation process and the subsequent ecological monitoring as part of the Dirk Hartog Island National Park Ecological Restoration Project (Cowen et al. 2021). Host species sampled were the greater stick-nest rat *Leporillus conditor* (Sturt, 1848), the sandy inland mouse *Pseudomys hermannsburgensis* (Waite, 1896), the Shark Bay Mouse *Pseudomys gouldii* (Waterhouse, 1839), and the house mouse *Mus musculus* Linnaeus, 1758. Localities sampled were Northwest Island (20° 21' 46"S, 115° 31' 30"E), Dirk Hartog Island (25° 49' 17"S, 113° 04' 46"E), Salutation Island (26° 32' 22"S, 113° 46' 04"E), and Bernier Island (24° 52' 03"S, 113° 08' 37"E).

Specimens were cleared in Nesbitt's solution and mounted in Hoyer's medium following Walter and Krantz (2009). The slides are deposited in the Western Australian Museum, Perth and the Australian National Insect Collection, Canberra. Mites were identified according to Domrow (1988). Terminology follows Lindquist and Evans (1965) (dorsal idiosoma chaetotaxy), Evans and Till (1965) (leg chaetotaxy) and Evans and Till (1979) (general anatomy).

RESULTS

Laelaps lybacia Domrow, 1979

Figures 1–5

Laelaps lybacia Domrow, 1979: 203.

Laelaps lybacia.— Domrow, 1988: 839.

MATERIAL EXAMINED

Australia: ***Western Australia***: 3 ♀, 4 ♂, Northwest Island, on *Pseudomys gouldii*, 20–22 April 2021; 13 ♀, 14 ♂, Bernier Island, on *P. gouldii*, 28 April to 2 May 2022.

Male

Dorsal idiosoma: Dorsal shield length 680–720 mm, width 530–560 µm (n=5), surface smooth but with distinct sigilla (Figure 1). Podonotal section with 19 pairs of setae; *j1* longest, 42–45 µm, *j2* 30 µm, others minute; *z3* absent. Opisthonotal section with 14 pairs of setae; *Z5* longest, 55–65 µm, *J5* short, 12–15 µm, others 20–30 µm, S3 absent; posterolateral region of shield with two pairs of large conspicuous gland pores.

Ventral idiosoma (Figure 2): Tritosternum with base 35 µm long, lightly pilose laciniae 140 µm long, base flanked by a pair of minute lenticular sclerites. Presternal area ornamented with a series of faint curved lines. Sternal, genital, and anal shields fused to form a large shield bearing ten pairs of setae and three circum-anal setae, two pairs of lyrifissures, and two pairs of gland pores; its surface ornamentated with a pattern of polygons, weaker and irregular between coxae IV; strongly-developed sigilla between coxae III and IV. Genital opening in anterior margin of sternal shield, its anterior margin open. Setae *st1–st5* very long and conspicuous, each reaching well past the base of the following seta, length 80–100 µm. Opisthogastric section of shield with five pairs of setae, length 55–80 µm; anus surrounded by a lightly sclerotised

area of cuticle; para-anal setae 15–20 µm, inserted at posterior level of anus, post-anal seta 32–35 µm; anterior ends of cribrum projecting only slightly anterior to post-anal seta. Stigmata at the anterior level of coxa IV, peritreme narrow, reaching forward to anterior level of coxa I. Narrow parapodal plate embracing coxa IV, irregular and variable metapodal plate present behind coxa IV; opisthogastric cuticle lateral to ventri-anal shield with two pairs of long setae.

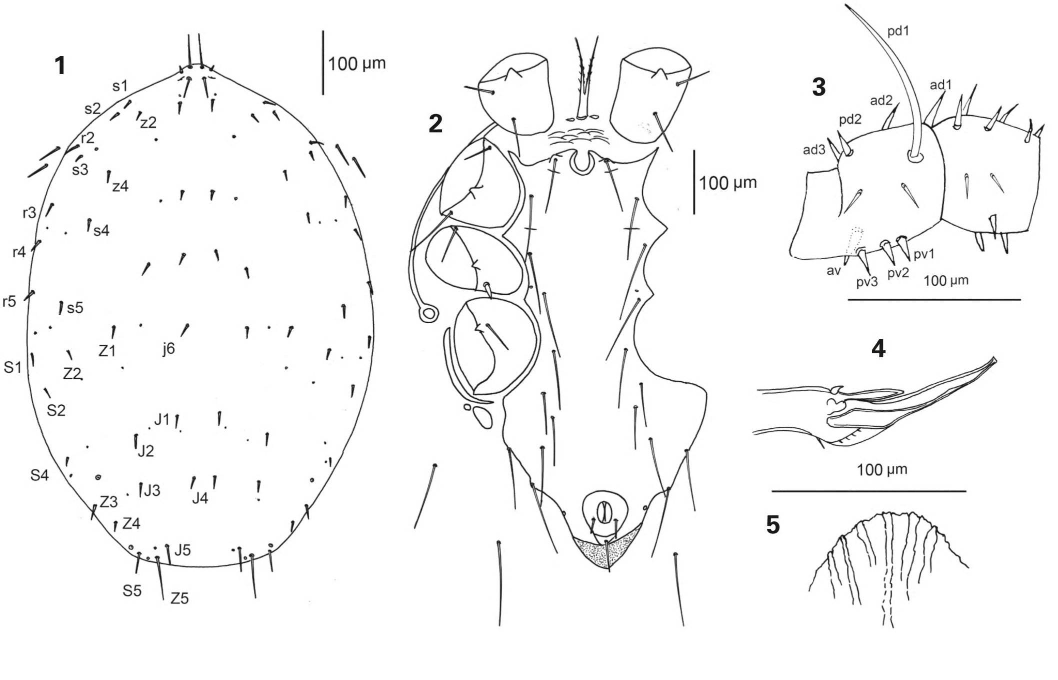
Legs: All tarsi with well-developed ambulacrum and a pair of claws, those on tarsus I smallest. Leg IV longest (820–850 µm), longer than idiosoma, other legs shorter than idiosoma. Chaetotaxy: Leg I: coxa 0 0/1 0/1 0 (*av* displaced posteriorly, much longer than *pv)*, trochanter 1 0/2 1/1 1, femur 2 3/1 2/3 2 (ventral setae displaced laterally, thick, blunt, spine-like; *pd1* greatly elongated, Figure 3), genu 2 3/2 3/1 2 (dorsal setae thick, blunt, spine-like), tibia 2 3/2 3/1 2. Leg II: coxa 0 0/1 0/1 0 (*pv* much longer and thicker than *av*), trochanter 1 0/2 0/1 1, femur 2 3/1 2/2 1 (ventral setae thick, blunt, spine-like), genu 2 3/1 2/1 2 (ventral setae thick, blunt, spine-like), tibia 2 2/1 2/1 2 (ventral setae thick, blunt, spine-like), tarsus 3 3/2 3/2 3 + *mv*, *md*, *al2* and *pl2* very long and thick. Leg III: coxa 0 0/1 0/1 0 (*pv* short, thick, spine-like), trochanter 1 0/2 0/1 1, femur 1 2/1 1/0 1, genu 2 2/1 2/1 1 (*pv* short, thick, spine-like), tibia 2 1/1 2/1 1 (*pv* short, thick, spine-like), tarsus 3 3/2 3/2 3 + *mv, md*. Leg IV: coxa 0 0/1 0/0 0, trochanter 1 0/2 0/1 1, femur 1 2/1 1/0 1, genu 2 2/1 3/0 1, tibia 2 1/1 3/1 2, tarsus 3 3/2 3/2 3 + *mv, md*.

Gnathosoma: As for female except movable digit of chelicera with very long upturned spermatodactyl, arthrodial membrane with a series of short filaments; fixed digit reduced, membranous, with bluntly tapering tip; dorsal seta robust, curved (Figure 4).

NOTES

Laelaps lybacia was described from the Shark Bay mouse on Bernier Island. It was previously known only from one female specimen. The females examined here agree with the description and illustrations in Domrow (1979, 1988). The male is described here for the first time. The male described here is identified as that of *L. lybacia* on the grounds of its association with females of *L. lybacia*. On five occasions males of the type described here were found on the same individual host as females of *L. lybacia*, with no other mites present. Most of the setae on the dorsal shield of the male are longer than the corresponding setae in the female.

Domrow (1979) did not describe the epistome of *L. lybacia*, but described that of the related species *L. janalis* as 'soft and diaphanous, apparently with two small lobes in median indentation', and that of *L. bycalia* as having 'four small weak median lobes'. The epistome of *L. lybacia* is not visible in most of the specimens examined here, but can sometimes be seen as an unsclerotised membranous arch, with a series of radiating lobes (Figure 5). Domrow (1979) described 19 pairs of podonotal setae and 14 opisthonotal pairs in the female, with *z3* and *S3* absent, and that interpretation is provisionally accepted here (Figure 1).



FIGURES 1–5 *Laelaps lybacia.* 1) male, dorsal idiosoma; 2) male ventral idiosoma; 3) male, leg I femur and genu, posterior face; 4) male, chelicera; 5) female, epistome.

Laelaps rothschildi Hirst, 1914

Laelaps rothschildi Hirst, 1914: 325.

Laelaps melomys Womersley, 1937: 534 (synonymy by Domrow and Smith, 1956).

Laelaps rothschildi.— Domrow, 1956: 202; Domrow, 1965; 19; Domrow, 1977: 215; Domrow, 1988: 840.

MATERIAL EXAMINED

Australia: *Western Australia*: 30 ♀, 2 deutonymphs, Salutation Island, on *Leporillus conditor*, 19–21 May 2021.

NOTES

The female specimens identified as *Laelaps rothschildi* are consistent with the key to species of *Laelaps* in Domrow (1988) — dorsal shield setae short, not reaching next posterior seta; setae *px2* and *px3* present; posterior seta on coxa II fine and pointed; posterior seta on coxa III thick, blunt, spur-like; genitoventral shield greatly expanded behind coxae IV, its lateral margins sinuous, widest between third pair of setae, ratio of its width to length behind genital setae 2.0, distance between fourth pair of setae greater than width of anal shield, posterior margin of genitoventral shield concave, partly enclosing anal shield. The deutonymphs agree well with the description and illustration in Domrow (1977).

Domrow (1973) compared *L. rothschildi* with the related species *L. aella* Domrow, 1973. These two species differ in the shape of the genitoventral and anal shields. The post-anal seta is inserted in the normal sclerotised area of the anal shield in *L. rothschildi*, but in unsclerotised cuticle in *L.aella*. Seta *pd1* on femur II is longer than surrounding setae in *L. aella*, much more strongly so in *L. rothschildi*.

Domrow (1962, 1967, 1973) referred to an apparent giant variety of *L. rothschildi* that occurs on the giant white-tailed rat *Uromys caudimaculatus* (Krefft 1867) in north Queensland, and whose taxonomic status remains unresolved. In the specimens examined here the dorsal shield measures 924–1016 µm long x 609–680 µm wide (n=10), which is consistent with the length 0.95–1.2 mm orginally described for *L. rothschildi* by Hirst (1914) and the 1.2 mm for its synonym *L. melomys* Womersley, 1937.

Laelaps rothschildi occurs in northern Australia from 'coastal N. Australia (The Kimberley to SE. Queensland, including Atherton Tableland)' (Domrow 1988). Its hosts include multiple species of rodents and marsupials. The specimens examined here indicate a significant southward extension of its known range in Western Australia, and the first record of its occurrence on *Leporillus conditor*. This species of host was once widespread in semi-arid areas of southern Australia, but was reduced to a population on the Franklin Islands of South Australia following European settlement (Short et al. 2019). That population formed the basis of a captive breeding program followed by re-introduction to a range of sites including Salutation Island. This dramatic disruption of the biogeography of *L. conditor* may have had unpredictable effects on the biology of its parasites, and may have included contact with other species of hosts in captivity.

Laelaps spatanges Domrow, 1973

Laelaps spatanges Domrow, 1973: 73.

Laelaps spatanges.— Domrow, 1988: 841.

MATERIAL EXAMINED

Australia: *Western Australia*: Dirk Hartog Island: 8 ♀, on *Pseudomys hermannsburgensis*, 13 May 2021 to 10 May 2022; 1 ♀, on *Mus musculus*, 23 May 2021.

NOTES

The females identified as *Laelaps spatanges* are consistent with the key to species of *Laelaps* in Domrow (1988) — dorsal shield setae *px2* present, *px3* absent; dorsal shield setae long, J5 projecting well beyond posterior margin of shield; genitoventral shield narrow, fourth pair of setae inserted in its postero-lateral corners; posterior seta on coxa I not spinose. The male is not known and was not present in the material examined here.

Laelaps spatanges has been recorded on several species of *Pseudomys* from scattered localities in northern Australia (Domrow 1973, 1988; Weaver and Smales 2012), and on *Pseudomys pilligaensis* in Taronga Zoo (Domrow 1992). The specimens examined here indicate a significant southward extension of its known range in Western Australia.

Mesolaelaps australiensis (Hirst, 1926)

Laelaps (*Mesolaelaps*) *australiensis* Hirst, 1926: 840.

Mesolaelaps australiensis.— Domrow, 1956: 203; Domrow, 1988: 8.

MATERIAL EXAMINED

Australia: *Western Australia*: 1 ♀, Bernier Island, 28 April 2022, on *Pseudomys gouldii*.

NOTES

Mesolaelaps australiensis is very abundant and widespread in Australia and neighbouring countries on a wide variety of hosts, including birds and their nests, lizards, marsupials, and rodents (Domrow 1979, 1988). Its host range is now extended further to include *Pseudomys gouldii*. Previous records in Western Australian include several sites in the Kimberley and Mitchell Plateau, and the Wanjarri Nature Reserve (near Wiluna), inland from Shark Bay. The specimen examined here is in excellent agreement with the descriptions and illustrations in Hirst (1926) and Domrow (1988).

DISCUSSION

The females of the species discussed here are easily distinguished from each other. *Mesolaelaps australiensis* has four pairs of ventral setae on tibia I, while all the species of *Laelaps* have three. In *Laelaps rothschildi* the anal shield is wider than long, and is embraced by the concave posterior margin of the genital shield (Hirst 1914). In *L. lybacia* and *L. spatanges* the anal shield is longer than wide, and clearly separated

from the genital shield (Domrow 1973, 1979). In *L. lybacia* the genital shield has a broad, slightly concave posterior margin and bears four pairs of setae, two of which are minute (Domrow 1979). In *L. spatanges* the genital shield has a rounded and convex posterior margin and bears four pairs of very long setae (Domrow 1973). In *L. spatanges* the dorsal shield setae are very long and conspicuous, long enough to reach past the next posterior seta (Domrow 1973). In *L. rothschildi* and *L. lybacia* these setae are minute (Domrow 1963, 1979).

The results presented here add further information about the host range of the studied mites. *Laelaps rothschildi* was found on *Leporillus conditor*, which appears to be the first record of a parasitic mite on this host. *Laelaps spatanges* was found on its previously-known host *Pseudomys hermannsburgensis* and on *Mus musculus*; *Pseudomys gouldii* is a new host record for *Laelaps lybacia*. Only one of the hosts examined was found to carry two species of Laelapidae — one of the specimens of *Pseudomys gouldii* carried one specimen of *Laelaps lybacia* and one specimen of *Mesolaelaps australiensis*.

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ANIMAL ETHICS STATEMENT

All sampling was conducted as approved by and in accordance with the Murdoch University Animal ethics committee (RW 3307/21; RW3215/20; RW3305/21, Cadaver 713), and Department of Biodiversity, Conservation and Attractions (DBCA) ethics committee (2021-03A; 2021-08A; 2019-23A) and DBCA permits (TFA2021-0035, F025000276).

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SHORT COMMUNICATION

Bats detected at Roleystone, Western Australia

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INTRODUCTION

Micro bats had been seen foraging under streetlights and occasionally found dead as a result of vehicle collisions in Roleystone, suburban Perth or in the case of the white-striped free-tailed bat (*Austronomus australis*), heard passing overhead. The aim of the study was to determine which species were present in the area and in which season of the year, using bat call identification.

METHODS

The study site, located at -32.1127°S, 116.0775°E was in a garden setting in Roleystone, a residential suburb of Metropolitan Perth located some 30 km southeast of the CBD, near the margin of the Darling Scarp in the Jarrah Forest bioregion, in Western Australia. Residential blocks are mostly about 2000 m^2 (0.2 ha) and many retain remnants of the original forest tree flora, principally the Myrtaceous species, Jarrah, *Eucalyptus marginata* and Marri, *Corymbia calophylla* although cultivated, non-locally indigenous, eucalypts, and exotic trees are common. Understories largely comprise cultivated shrubs, including Australian natives and exotic species. The insertion of houses and other structures including roads, has created gaps in the tree canopy. Small reserves of approximately 2 ha, that retain examples of the original flora are scattered throughout the area, with one within 400 m of the study site.

The study was undertaken between January 2021 and May 2023. Wildlife Acoustics Songmeter full spectrum ultrasonic recorders (a SM2BAT coupled to a SMX-US omnidirectional ultrasonic microphone, and a SMminiBAT, which has an internal microphone) set to a sampling rate of 384 kHz were used to capture and record bat ultrasonic pulse sequences (Table 1). The detectors were attached to wooden poles <1 m above ground level and were not directly influenced by street lighting. Both recorders were activated from dusk to dawn for three successive nights. The location of the SM Mini detector was changed by about 5 m in 2023 to avoid developing overhead vegetation clutter. To avoid damaging equipment, detectors were not deployed on nights when rain was forecast. Kaleidoscope 5.6.0 (Wildlife Acoustics) was used to extract bat echolocation sequences from the recordings in pulse code modulation wave format (.wav). Syntrillium Cool Edit 2000, now Adobe Audition 2 (Adobe Systems, USA), was used to display each echolocation sequence in spectral view and measure pulse parameters such as peak frequency, fineness-of-tuning, duration, repetition rate and shape, as described in McKenzie et al. (2019, 2020). Sequences were identified to species against reference sequence data in the author's own library of calls and reported in Bullen and McKenzie (2002) and Webala et al. (2010).

RESULTS

Eight bat species were detected. Two were molossid species in the genera *Austronomus* and *Ozimops*. The remaining six species were Vespertilionids from four genera, *Chalinolobus*, *Falsistrellus*, *Nyctophilus* and *Vespadelus*, The species recorded and the seasons in which they were detected are shown in Table 2.

TABLE 1 The month, year and season when bat detectors were deployed and the detector model used on each occasion.

Date	Season	Detector model
2021 January	Summer	SM2 bat detector
2021 August	winter	SM2 bat detector
2021 October	Spring	SM2 bat detector
2021 December	Summer	SM2 bat detector
2022 July	Winter	SM2 bat detector
2022 June	Winter	SM2 bat detector
2022 November	Spring	SM Mini
2022 December	Summer	SM Mini
2023 March	Autumn	SM Mini
2023 April	Spring	SM Mini
2023 May	Autumn	SM Mini

TABLE 2 Bat species recorded: 'Aa' *Austronomus australis*; 'Cg' *Chalinolobus gouldii*; 'Cm' *Chalinolobus morio*; 'Fm' *Falsistrellus mackenziei*; 'Ok' *Ozimops kitcheneri*; 'Ng' *Nyctophilus geoffroyi*; 'Nh' *Nyctophilus holtorum*; 'Vr' *Vespadelus regulus*.

Dates (n=12)	Seasons (n=4)	Species	Aa	Cg	Cm	Fm	Ok	Nh	Ng	Vr
2021 Dec	Summer	6	1	1	*	1	1	*	1	1
2022 Dec	Summer	7	1	1	*	1	1	1	1	1
2021 Jan	Summer	7	1	1	1	1	1	*	1	1
2023 Mar	Autumn	4	*	1	*	*	1	*	1	1
2023 Apr	Autumn	4	*	1	*	*	1	*	1	1
2023 May	Autumn	4	*	1	*	*	1	*	1	1
2022 Jun	Winter	0	*	*	*	*	*	*	*	*
2022 Jul	Winter	3	*	1	*	*	1	*	*	1
2021 Aug	Winter	3	*	1	*	*	1	*	*	1
2021 Oct	Spring	6	1	1	*	1	1	*	1	1
2022 Nov	Spring	6	1	1	*	1	1	*	1	1
Totals			**5**	**10**	**1**	**5**	**10**	**1**	**8**	**10**

The presence of *N. holtorum* was based on two sequences recorded about an hour apart on the same night; each sequence comprised pulses between 49 and 53 kHz as well as a sub-sequence of three to four departure pulses at just over 60 kHz which distinguishes its search mode echolocation sequences from *N. major* and *N. geoffroyi* (Bullen and McKenzie 2002).

DISCUSSION

Maps showing the known distributions of Western Australian bats are available from Australian Bat Society (2021). All eight species detected were within their known ranges, although, *F. mackenziei* was at the northern edge of its known distribution. The study site is within the known range of only one Vespertilionid species that was not detected, *Nyctophilus major.*

The apparent absence of *A. australis* in autumn and winter is consistent with movements demonstrated by Bullen and McKenzie (2005) who showed that, in Western Australia the species is a partial migrant expanding its range northwards in autumn when temperatures and atmospheric enthalpy in tropical regions are falling, and contracting southwards in spring when those parameters increase. A similar seasonal pattern of presence-absence was evident in *F. mackenziei,* but clearly for different reasons as the study site is at the northern limit of its distribution. *C. morio* and *N. holtorum* were apparently rare as they were detected only once (in summer), but the other four species, *C. gouldii*, *N. geoffroyi*, *O. kitcheneri* and *V. regulus*, were detected on most occasions in all seasons.

Autumn and winter, when night temperatures were low, corresponded with detection of fewer foraging bat species probably because there was little reward for foraging on colder nights. Casual night time observations of insects attracted to outside lights at the study site (by ANS) showed more flying insects in the warmer months than in colder months, a pattern that corresponded with diversity of foraging bat species.

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Systematics and biogeography of Lesser Sunda paddy frogs (Dicroglossidae: *Fejervarya*)

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ABSTRACT – The Lesser Sunda Archipelago is one of the world's most tectonically complex regions and hosts a unique assemblage of amphibian species. Paddy frogs (genus *Fejervarya*) occur throughout the region, but the systematic position and distribution of each constituent species remains unclear. We present a set of comprehensive mtDNA and morphometric data on the three paddy frog species in the Lesser Sundas: *F. cancrivora*, *F. iskandari* and *F. verruculosa*. We clarify the phylogenetic position of *F. verruculosa*, placing it as the sister species of *F. cancrivora*. We also confirm that *F. iskandari* occur in the Lesser Sundas. Molecular data suggests that *F. cancrivora* is panmictic across Java and the Sunda Arc, while *F. verruculosa* and *F. iskandari* comprise multiple highly divergent populations within the Lesser Sundas. Phylogeographic results appear to support at least two natural colonisations of *Fejervarya* in the Lesser Sunda Archipelago, one by *F. iskandari* and one by *F. verruculosa*, whereas contemporary *F. cancrivora* populations likely arose from human-mediated movement. Our results demonstrate the biogeographic complexity of the Lesser Sunda Archipelago and identify key knowledge gaps in Lesser Sunda *Fejervarya*.

KEYWORDS: Amphibian, Mitochondrial DNA, Phylogeography, Species distribution, Wallacea

INTRODUCTION

The Lesser Sunda (LS) Archipelago is a chain of islands occupying the southern portion of Wallacea and home to biological communities distinct from neighbouring regions (Lohman et al. 2011; Ali and Heaney 2021). One factor leading to the region's biological distinctiveness is that the LS Archipelago draws upon fauna from two zoogeographic continents: the Oriental region of the Sunda Shelf, dominated by mainland Asian species; and the Australo-Papuan region of the Sahul Shelf, dominated by Australian species (Ali and Heaney 2021; White et al. 2021). The intermediate Wallacean region acts as a two-way filter, containing its own unique transitional species and facilitating two-way exchanges between zoogeographic continents (sensu Whittaker and Fernândez-Palacios 2007). Recent genetic studies revealed that a number of wide-ranging reptile and amphibian species from the region documented solely based on morphology (e.g. Kaiser et al. 2011; O'Shea et al. 2012) actually comprise multiple species with localised distributions (Reilly et al. 2019a, 2022a, 2022b, 2022c, 2023), suggesting that true herpetofaunal diversity of the region is underestimated.

Geologically, the LS Archipelago can be divided into four distinct regions: 1) the eastern end of the volcanic Sunda Arc (Bali, Lombok, Sumbawa, Flores); 2) Sumba Island, an anomalous continental plate fragment (Abdullah et al. 2000); 3) the western end of the Inner Banda Arc (IB), consisting of the volcanic

islands of Pantar, Alor, Atauro, and Wetar; and 4) the western end of the Outer Banda (OB) Arc, consisting of the islands of Rote, Timor, and several islands that lie east of Timor (Figure 1). Portions of the volcanic Sunda Arc islands are thought to have become continuously emergent beginning 10–12 million years ago, while Sumba and the Banda Arcs first arose 3–5 million years ago (Hall 2011). Several of the larger Sunda Arc islands including Sumbawa and Flores likely formed as separate islets before coalescing into the larger islands (Muraoka et al. 2005; Lohman et al. 2011; Reilly et al. 2019a, 2022c). The intricate geologic history of the LS Archipelago presents an intriguing model system of animal dispersal and vicariance. Dispersal pathways between LS islands are thought to be influenced by ocean currents from the Indonesian throughflow and surface wind patterns. However, movement between islands is supplemented by human-mediated dispersal, including components of the herpetofauna (Brown 2010; Linkem et al. 2013; Reilly et al. 2017, 2019b). Human-mediated dispersal was likely facilitated by a sea-faring culture in the LS Archipelago, which has existed in the region for the last 40,000 years (O'Connor et al. 2011).

The genus *Fejervarya* Bolkay, 1915 currently consists of 14 Asian ground frog species (Frost 2024), three of which are found in the Lesser Sundas: *F. cancrivora* (Gravenhorst, 1829), *F. verruculosa* (Roux, 1911) and *F. iskandari* Veith et al., 2001. *Fejervarya cancrivora* are found throughout South-East (SE) Asia (Yodthong et al. 2019a), while *F. verruculosa* appears to be restricted to the Lesser Sunda (LS) archipelago and is morphologically similar to *F. cancrivora* (van Kampen 1923). *Fejervarya iskandari* was described by Veith et al. (2001) from West Java and was referred to as a Java Island endemic but has subsequently been found to occur in the LS Archipelago (Hasan et al. 2022). Taxonomic and phylogeographic relationships of *Fejervarya* west of Wallace's Line (Figure 1) has been thoroughly examined (Dubois and Ohler, 2000; Veith et al. 2001; Kotaki et al. 2008, 2010; Kurniawan et al. 2010, 2014; Köhler et al. 2019; Yodthong et al. 2019a), whereas *Fejervarya* east of Wallace's Line remains poorly understood with imprecisely-known species distributions. This is due to limited sampling in the LS Archipelago and the morphological conservatism of frogs of the genus *Fejervarya*, which makes species assignment challenging.

This study uses molecular and morphological data to delineate phylogeographic structure and systematic relationships of the three LS *Fejervarya* species, while evaluating the intraspecific molecular and morphological diversity. We also use our findings to hypothesise how both dispersal and human-mediated introduction explains the contemporary distributions of LS *Fejervarya* lineages.

MATERIALS AND METHODS

SAMPLE COLLECTION

Institutional acronyms: Western Australian Museum, Perth (WAM); Museum of Vertebrate Zoology, Berkeley (MVZ); Museum Zoologicum Bogoriense, Bogor (MZB); Institut Teknologi Bandung, Bandung (ITB).

Fejervarya tissues and vouchers were obtained from two sets of field surveys: one set conducted by WAM and MZB between 1988 and 1991 and another set conducted by MVZ, MZB, and ITB between 2010 and 2013 (Figure 2). This study uses both tissues and vouchers from the WAM 1988–1991 survey but only tissues (not vouchers) from the MVZ/MZB 2010–2013 surveys. All vouchers are housed at WAM or MVZ (Appendix Table 1). Liver, muscle, or heart tissues were obtained from specimens prior to formalin-fixation and stored in 70% ethanol or RNAlater in transit to WAM/MVZ. No audio recordings (site or individual) were taken. All vouchers were identified to species based on morphology or left unidentified and housed as *Fejervarya* sp. in their respective institutions.

MOLECULAR ANALYSES

Genomic DNA was extracted from liver tissue using either a salt extraction technique or using a Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, California, USA). Mitochondrial CO1 gene sequences were generated from 329 WAM specimens by the University of Guelph (Ontario, Canada). A preliminary CO1 tree was generated in Barcode of Life Data (BoLD) Systems, version 4 (Ratnasingham and Hebert 2007; https://www.boldsystems.org/). Individuals with sequences of <200 bps were removed from the tree, leaving a total of 303 CO1 sequences. A portion of the 16S ribosomal RNA gene was PCR-amplified for all MVZ samples as well as a subset of 25 WAM specimens representing each major clade identified from preliminary analyses of the CO1 dataset. The 16S gene was amplified using the primers 16sc-L (5'-GTRGGCCTAAAAGCAGCCAC-3') and 16sd-H (5'-CTCCGGTCTGAACTCAGATGACGTAG- 3') (Palumbi et al. 2002). PCR products were purified using ExoSAP-IT (USB, Cleveland, Ohio, USA) before being sequenced in both directions using cycle sequencing reactions with BigDye v3.1 (Applied Biosystems, Foster City, California, USA). The cycle sequencing reactions were then cleaned by ethanol precipitation before being sequenced on an ABI 3730 sequencer (Applied Biosystems). CO1 and 16S sequences from the same individuals were concatenated in GENEIOUS v11.1.5 (Biomatters Ltd.).

To place our samples into a broader phylogenetic context, additional 16S and CO1 sequence data from GenBank were downloaded for lineages of *Fejervarya cancrivora*; *F. iskandari*; *F. kawamurai* Djong et al., 2011; *F. limnocharis* (Gravenhorst, 1829); *F. moodiei* (Taylor, 1920); *F. multistriata* (Hallowell, 1861); and an

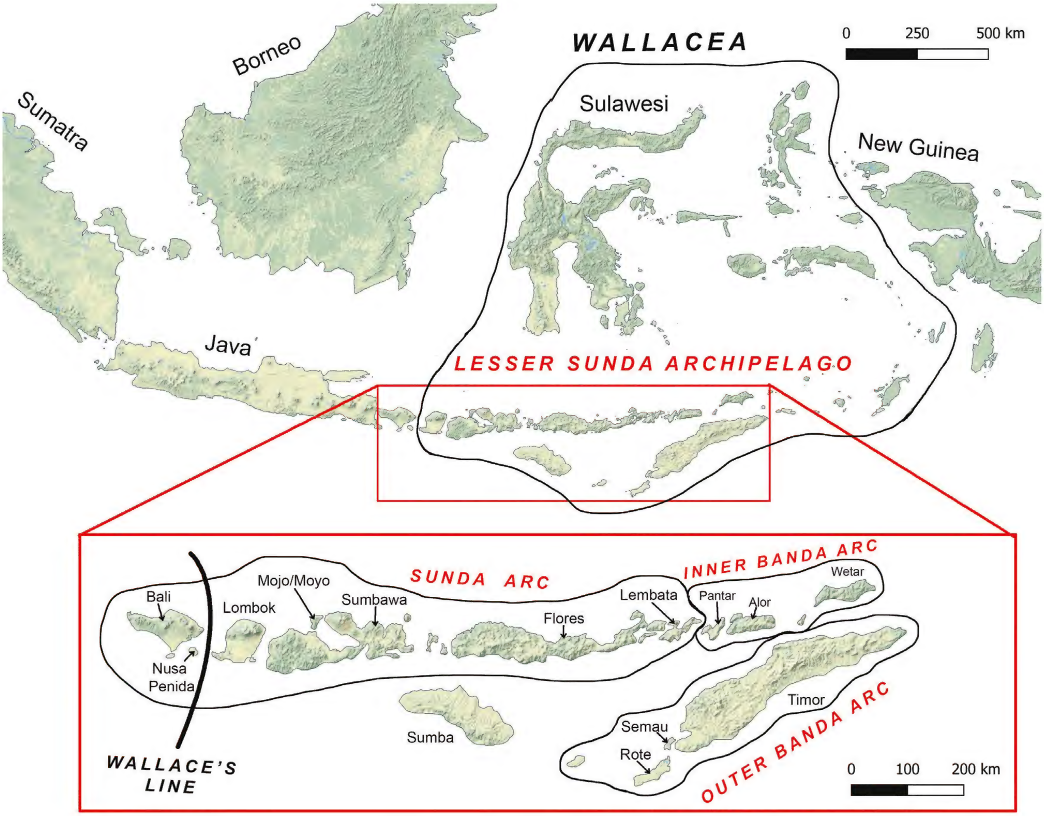

FIGURE 1 Map of Wallacea and the Lesser Sunda Archipelago (inset, within red box). All three island arcs and Wallace's Line extend beyond the Lesser Sundas, but these areas are not depicted in the inset map. Note: Sumba is not a part of an island arc but an anomalous continental fragment (Abdullah et al. 2000).

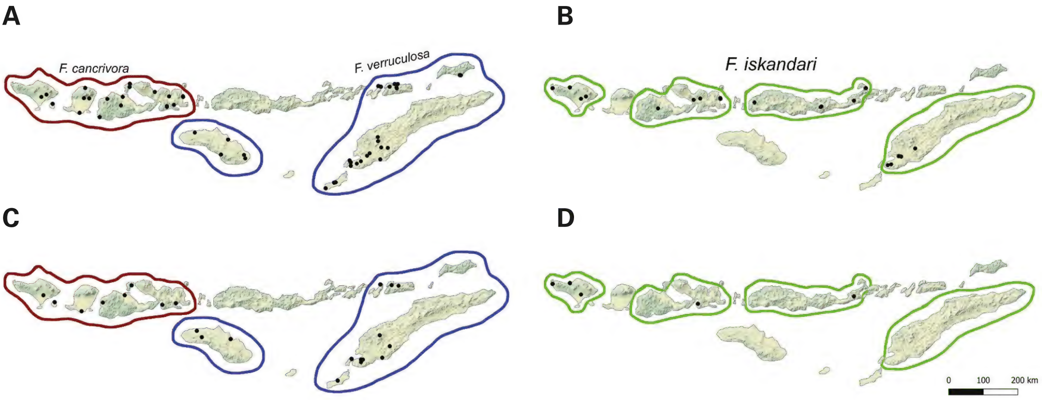

FIGURE 2 Molecular sampling localities: A) *Fejervarya cancrivora* (brown) + *F. verruculosa* (blue); B) *F. iskandari* (green). Morphological sampling localities: C) *F. cancrivora* (brown) + *F. verruculosa* (blue); D) *F. iskandari* (green).

outgroup of *Hoplobatrachus tigerinus* (Daudin, 1802) (Sumida et al. 2002; Chen et al. 2005; Liu et al. 2005; Che et al. 2007, 2009; Kotaki et al. 2008, 2010; Ren et al. 2009; Alam et al. 2010; Kurniawan et al. 2010, 2014; Matsui et al. 2010; Cheng et al. 2018; Jiang et al. 2020; Flury et al. 2021; Zhang et al. 2021) including sequence data from introduced and commercially-harvested *F. cancrivora* (Wostl et al. 2016; Ohler and Nicolas, 2017). These sequences are listed in Appendix Table 2. Taxonomic assignments of outgroup sequences follow the Yodthong et al. (2019a, 2019b) revision and corrigenda of mainland SE Asia *F. cancrivora* populations. GenBank sequences AB444963 and EU979849 were re-attributed to a divergent lineage within the *F. cancrivora* group which is commonly considered to be an undescribed species (Kurniawan et al. 2010; Yodthong et al. 2019a). We have followed these sources and treated them as the Sulawesi- (or Pelabuhan Ratu-) *F.* cf. *cancrivora*. The outgroup sequences DQ45822, AF206473, AB070738 (directly reassigned in Yodthong et al. 2019b), alongside sequences that group with these individuals were attributed to *F. moodiei*. MW007342 (Borneo) is sister to and well-diverged from *F. moodiei*, suggesting that it represents an undescribed species of Bornean *Fejervarya*. These sequences were aligned with Clustal Omega (Sievers et al. 2011) with a final alignment length of 1601 bp containing 506 *Fejervarya* samples, 462 of which are from the Lesser Sundas. All newly generated 16S sequences have been deposited in GenBank (accession numbers: OP984408–OP984466, OP984467–OP984614, OP995445–OP995471).

TABLE 1 Morphometric sampling by island. Cells left blank indicates that species does not occur on island.

	F. cancrivora	*F. iskandari*	*F. verruculosa*
Bali	3	11	
Nusa Penida	7		
Lombok	1		
Mojo	1		
Sumbawa	6	3	
Flores		2	
Pantar			1
Alor			4
Wetar			0
Sumba			6
Rote			6
Semau			3
Timor		0	13
Total	**18**	**16**	**33**

Maximum Likelihood (ML) phylogenetic analysis was performed using the software IQ-TREE v1.6.12 (Nguyen et al. 2015) with model selection (model TIM2+F+I+G4) according to Bayesian information criterion (BIC) scores (Kalyaanamoorthy et al. 2017). Nodal support was determined with 1,000 ultrafast bootstrap replicates (UFBoot; Hoang et al. 2017) and 1,000 replicates of the single branch test (SH-aLRT). DNA alignments and full results files from IQ-TREE are found in the DRYAD digital repository (Reilly 2024). Based on the phylogeographic lineages found within *F. iskandari* and *F. verruculosa*, we obtained rough estimates of lineage divergence times using the Bayesian phylogenetic software BEAST2 v2.7 (Bouckaert et al. 2019). We chose a subset of samples representing the major mitochondrial lineages identified by the ML analysis and chose samples with both genes sequenced when available. The program was run under the GTR+G model of sequence evolution, which was the highest supported model from IQ-TREE implemented in BEAST2. Because we are examining intrageneric divergence, we used a strict molecular clock model assuming a rate of 1.3% lineage divergence per million years (estimated for the 16S gene in a group of ranid frogs; Macey et al. 2001). Two separate analyses were run for 50 million generations, sampled every 5,000 generations. After completion the log files were viewed in TRACER v1.7 (Rambaut et al. 2018) to confirm that parameters had converged by checking that the effective sample size (ESS) values for each parameter were greater than 200. Both runs were confirmed to have converged on the same posterior distribution. After discarding 25% of the samples as burn-in from each of the two runs, the remaining 15,000 trees were combined to generate a maximum clade credibility tree for which the branch lengths represent time, specifically millions of years ago (Ma). DNA alignments, log files and tree files are found in the DRYAD digital repository (Reilly 2024).

Sequence divergence between phylogeographic lineages were estimated by uploading the concatenated alignment on the web server DIVEIN (Deng et al. 2010) and calculated using PhyML v3.0 (Guindon et al. 2010). Mean uncorrected divergence levels were based on pairwise distances calculated with a GTR substitution model and four substitution rate categories.

MORPHOLOGICAL COMPARISONS

Morphological characters were measured for 67 sexually mature WAM *Fejervarya* specimens (Table 1) using MITUTOYO Absolute Coolant-Proof IP67 0-150 mm digital callipers. Sexual maturity was identified by the presence of secondary sexual characteristics. Adult male *F. cancrivora* and *F. verruculosa* were identified by the presence of paired dark triangular gular blotches,

while adult male *F. iskandari* were identified by the presence of paired grey vocal sacs on both sides of the mandible or a brown-grey streak forming a loose 'M'-shape across the throat. Females of all three species were identified by the presence of eggs. Foot webbing was examined following the notation used in Savage and Heyer (1967) following Veith et al. (2001) and Yodthong et al. (2019a).

Measurements: snout-vent length (SVL) — distance between snout tip and vent; head length (HL) — distance between snout tip and inner edge of tympanum, measured from dorsal midline; head width (HW) — measured level with anterior edge of tympana; snout-tympanum length (STL) — distance between snout tip and posterior edge of tympanum, measured obliquely; interocular distance (IOD) — distance between each eye measured along anterior of each eye opening; eye diameter (EYD) — measured between anterior- and posterior-most point of eye opening; internares distance (IND) — distance between each nares measured along anterior of each nares; tympanum-eye distance (TED) — distance between inner edge of tympanum and posterior of eye opening; tympanum diameter (TYD) — measured at midpoint level; upper arm length (UAL) — distance between base of limb to elbow, measured from the ventral surface; forearm length (FAL) — distance between elbow to midpoint between third and fourth palmar tubercles; forelimb length (FLL) — sum of upper arm and forearm lengths; hand length (HAL) — distance from midpoint between second and third palmar tubercles to tip of Finger III; thigh length (THL) — distance between groin fold and start of patella, measured parallel to femur; tibia length (TIL) — distance between end of patella and ankle; hindlimb length (HLL) — sum of thigh and tibia lengths; tarsus and foot length (TFOL) — distance between ankle and tip of Toe IV. Snout-vent length (SVL) was measured to the nearest millimetre, while all other characters were measured to the nearest 0.1 mm. Mensural values were standardised as a ratio (r) against SVL to adjust for size variation (e.g. rHL = relative head length; HL/SVL). Principal component analysis (PCA) among species was performed separately by sex using FactoMineR (Lê et al. 2008; Husson et al. 2017) and its subsequent add-ons. This PCA methodology was repeated for the major lineages within *F. verruculosa* but not for *F. iskandari* since there were not enough samples of each divergent lineage of *F. iskandari* housed at WAM.

Kruskal-Wallis tests were performed on standardised morphological measurements and morphometric ratios (rHL/rHW, rIOD/rHW, rTYD/rEYD, rTED/rEYD, rFLL/rHLL, rUAL/rFAL, rHAL/FAL, rTHL/rTIL, rTFOL/rTIL) between species with females and males analysed separately. Mann-Whitney U-tests were performed to determine whether size differences between females and males of each species are statistically significant. Kruskal-Wallis and Mann-Whitney tests were not repeated for divergent lineages of *Fejervarya verruculosa* and *F. iskandari* since there were not enough samples of both species from each island for meaningful statistical analysis. All statistical tests were performed in RStudio 2023.06.0 (RStudio Development Team 2023) with a significance threshold of 0.05.

RESULTS

TAXONOMIC ASSIGNMENTS

The ML phylogenetic estimate grouped all Lesser Sunda *F. cancrivora* together with all additional (including introduced and commercially harvested) *F. cancrivora* sequences, corroborating this species assignment. Lesser Sunda individuals belonging to the most inclusive monophyletic clade sister to *F. cancrivora* and grouping with *F. verruculosa* topotypes (Iliwaki, Wetar Island, Indonesia) were assigned to *F. verruculosa*. Individuals belonging to the most-inclusive clade with individuals from the type locality of *F. iskandari* (Cianjur, West Java, Indonesia; Veith et al. 2001), which is sister to *F. limnocharis* and *F. multistriata,* were assigned to *F. iskandari* following phylogenetic estimates in Djong et al. (2007, 2011) and Sanchez et al. (2018).

PHYLOGEOGRAPHIC STRUCTURES

Both ML and Bayesian phylogenetic trees recover *F. iskandari* as a well-supported monophyletic clade, and recover *F. verruculosa* as a monophyletic sister group to *F. cancrivora.* Intraspecific variation and biogeographic patterns vary between the three species (Figures 3–5). *Fejervarya cancrivora* is recovered as a monophyletic widespread lineage (BS [bootstrap value] = 98) (Figure 3). All Lesser Sunda individuals are recovered as part of this lineage, intermingled with samples from Malaysia, Taiwan, Sumatra, Java, Guam and commercially harvested *Fejervarya.* Private haplotypes from Sumbawa (BS = 81) and Nusa Penida individuals are nested within this lineage.

Unlike *F. cancrivora*, phylogeographic structure is present in both *F. iskandari* and *F. verruculosa. Fejervarya iskandari* is recovered as monophyletic (overall BS = 100; PP [posterior probability] = 1) and samples sort into three distinct clades (Figure 5). Samples from Java, Bali and Timor are only moderately supported as a single clade in the ML tree but are fully supported in the Bayesian tree (BS = 56; PP = 1). Sister to the Java + Bali + Timor clade is a Sumbawa + Flores clade (BS = 99; PP = 1), with well-supported Sumbawa (BS = 93; PP = 1) and Flores (BS = 100; PP = 1) sister groups. The split between the Java + Bali + Timor and the Sumbawa + Flores lineages is estimated to have occurred ~5 Ma and they are ~4.6% divergent from one another (Figure 5B; Table 2). The Sumbawa and Flores lineages are estimated to have diverged ~2 Ma and the mean divergence between them is ~2.2% (Figure 4; Table 2).

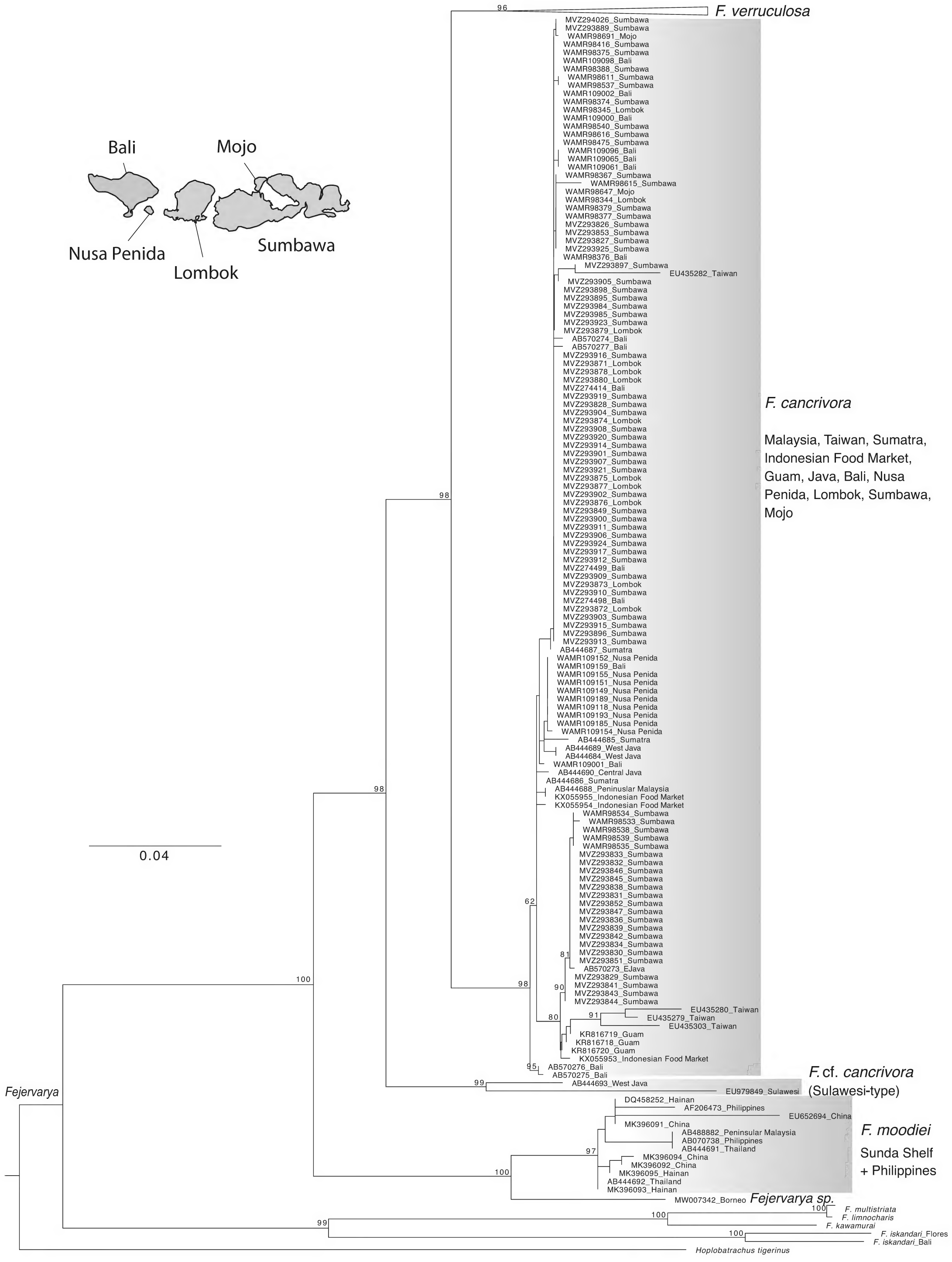

FIGURE 3 Maximum Likelihood majority rule consensus phylogeny of the CO1 and 16S mitochondrial genes for *Fejervarya cancrivora* samples. Numbers at nodes represent bootstrap support.

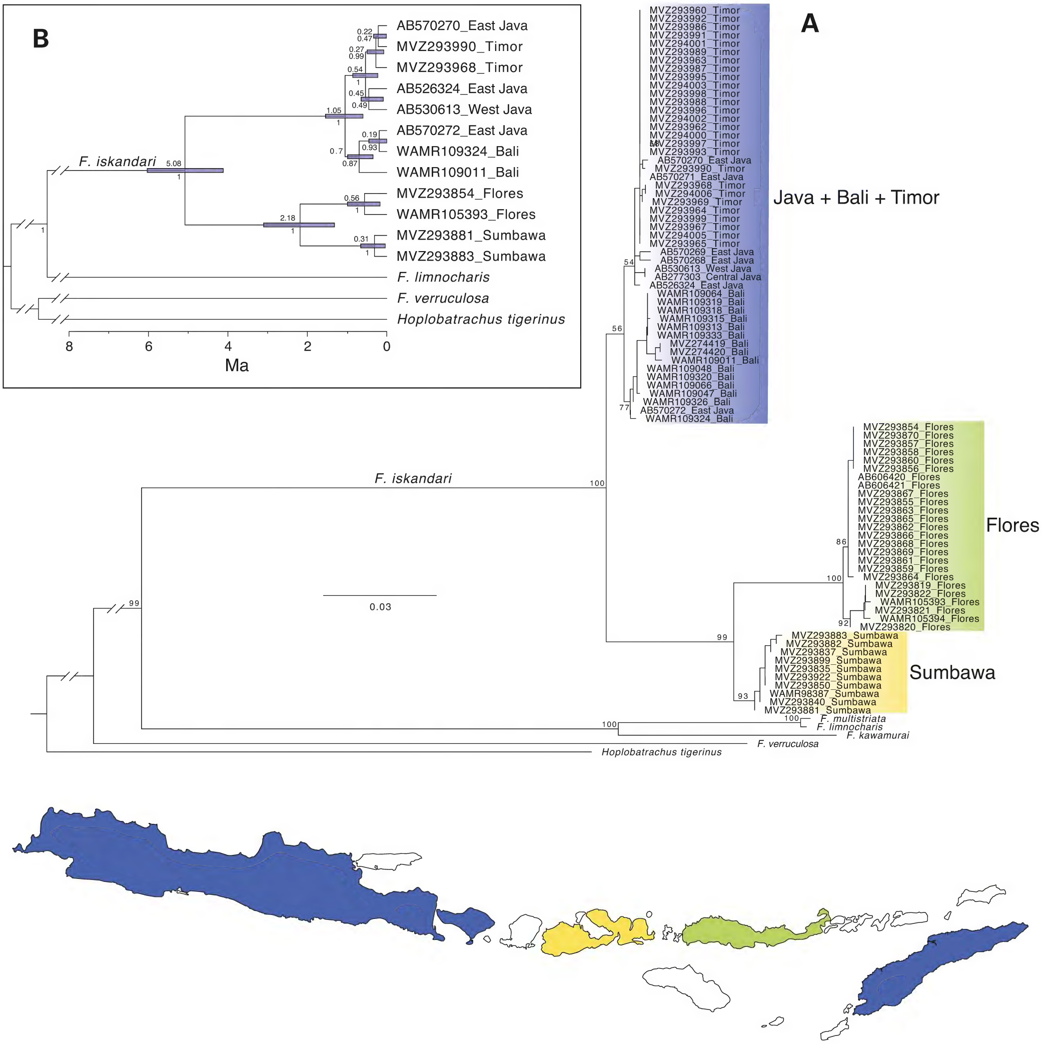

FIGURE 4 Phylogenies of the concatenated CO1 and 16S mitochondrial genes for *Fejervarya iskandari* samples: A) Maximum Likelihood majority rule consensus phylogeny where numbers at nodes represent bootstrap support; B) Bayesian time-calibrated phylogeny for a subset of samples representing the major clades. Note: numbers above nodes represent mean node ages and numbers below nodes represent posterior probability support.

Fejervarya verruculosa is monophyletic and sister to the *F. cancrivora* clade (overall BS = 96; PP = 1), and composed of three well-supported subclades: 1) an early-diverging Rote lineage (BS = 100; PP = 1); 2) a Sumba lineage (BS = 99; PP = 1); and 3) a Banda Arcs (Timor, Semau, Alor, Pantar, and Wetar) lineage (BS = 100; PP = 0.83) (Figure 4). The Sumba lineage is the sister to the Banda Arcs lineage (BS = 100; PP = 1), with the latter clade composed of multiple weakly divergent phylogeographic groups. The only monophyletic island population within the Banda Arcs clade is Wetar (BS = 99), though they are minimally divergent (note: Wetar Island is the type locality of *verruculosa*; Roux 1911). Populations from Alor, Pantar, Timor and Semau were each recovered as paraphyletic. PhyML divergence of concatenated sequences shows the Rote lineage is approximately 8% divergent on average from all other *F. verruculosa* and is estimated to have diverged ~5.4 Ma, while the Sumba lineage is approximately 6% divergent from the Banda Arcs lineage and is estimated to have diverged from it ~3 Ma (Figure 5; Table 2).

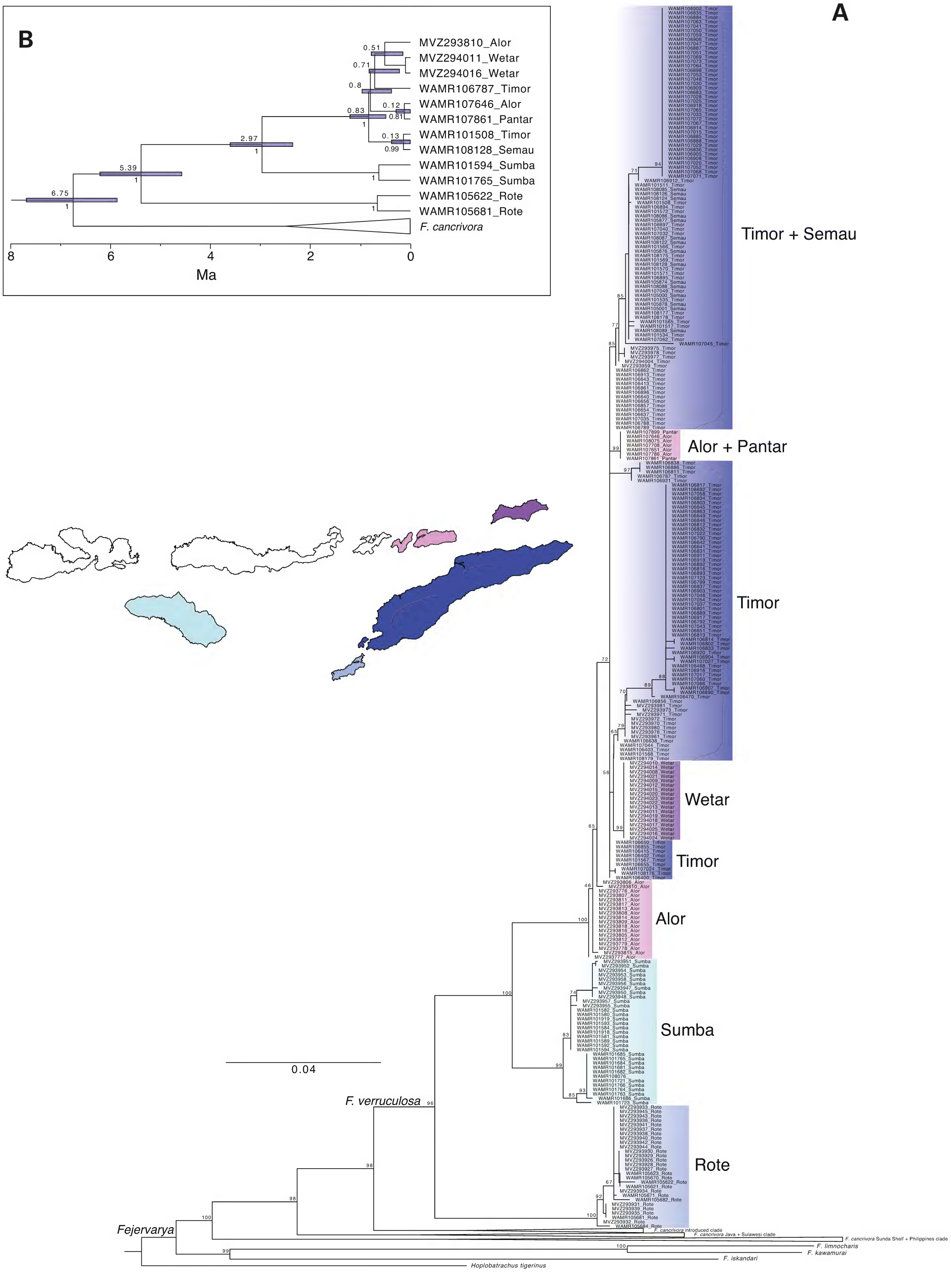

FIGURE 5 Phylogenies of the concatenated CO1 and 16S mitochondrial genes for *Fejervarya verruculosa* samples. A) Maximum Likelihood majority rule consensus phylogeny where numbers at nodes represent bootstrap support; B) Bayesian time-calibrated phylogeny for a subset of samples representing the major clades. Numbers above nodes represent mean node ages and numbers below nodes represent posterior probability support.

TABLE 2 Mean uncorrected divergences between divergent populations of *Fejervarya iskandari* and *F. verruculosa* analysed from concatenated alignment containing both CO1 and 16S genes. Divergence values presented as proportions.

	Java + Bali + Timor (n = 50)	Sumbawa (n = 10)	Flores (n = 25)	Rote (n = 28)	Sumba (n = 33)	Banda Arcs (n = 216)
F. iskandari						
Java + Bali + Timor	0	0.042	0.048	-	-	-
Sumbawa	0.042	0	0.022	-	-	-
Flores	0.048	0.022	0	-	-	-
F. verruculosa						
Rote	-	-	-	0	0.080	0.086
Sumba	-	-	-	0.080	0	0.063
Banda Arcs	-	-	-	0.086	0.063	0

MORPHOLOGY

PCA analysis between LS *F. cancrivora*, *F. iskandari* and *F. verruculosa* separated by sex revealed minimal morphological differences. There is considerable overlap between *F. cancrivora* and *F. verruculosa* across both sexes, while *F. iskandari* did not overlap with the rest of the samples with the exception of a single outlier male voucher (Figures 6A–B). The first three principal components (PCs) accounted for 64.7% and 65.9% of observed variance in females and males, respectively (Table 3). SVL mirrors species clusters in both correlation circles for females and males, suggesting that body size is the primary distinguishing characteristic between the three species (Figures 6C–D). Observed differences in SVL were more pronounced in females (cos-squared [$\cos^2$] value: 0.040 in PC1, 0.688 in PC2) than in males ($\cos^2$ value: 0.234 in PC1, 0.338 in PC2). Female *F. cancrivora* are much larger than male *F. cancrivora,* which are approximately the same size as female *F. verruculosa*. Male and female *F. iskandari* are usually smaller than male *F. verruculosa* (Table 5). We only identified four *F. iskandari* males in the WAM collection. These were slightly smaller than their female counterparts, agreeing with previous descriptions (Veith et al. 2001). Mann-Whitney U-tests between female and male SVL were statistically significant in *F. cancrivora* (U-stat = 78, p = 0.008) and *F. verruculosa* (U-stat = 286.5; p < 0.0001), but not in *F. iskandari* (U-stat = 38; p = 0.100).

PCA analysis on divergent *Fejervarya verruculosa* populations (Rote, Sumba and Banda Arcs) separated by sex showed little morphological differentiation between clades except for a single outlying female from Rote (Figures 6E–H). Description of each measured character can be found in the main text. The first three PCs explained 70.0% and 69.7% of observed variance within female and male *F. verruculosa*, respectively (Table 3). Cos^2 values for in the first PC were generally higher in females than in males, but this can be attributed to the outlying female.

Descriptive statistics for all morphometric characters of adult females and males are presented in Table 4. Kruskal-Wallis tests between species were statistically significant in SVL in both sexes, reinforcing body size as the primary distinguishing characteristic between LS species. Most other morphometric characters were conserved between species. There were differences in dorsum rugosity between *F. cancrivora* and *F. verruculosa*, with long dorsal furrows on the former and raised, short oblong patches on the latter. Additionally, foot webbing between Toes III and IV in *F. iskandari* is more incised than *F. cancrivora* or *F. verruculosa* (see species accounts and Figures 7–11).

SPECIES ACCOUNTS

The combination of strong phylogenetic support, discontinuous geographic distribution and morphological differences provides multiple independent lines of evidence to recognise at least three current Lesser Sunda *Fejervarya* species. We provide new descriptions in this section, presented in chronological order of their original descriptions. Morphometric measurements are presented as relative to SVL (e.g. rHL = relative head length; see Materials and Methods). A history of synonyms for all three species can be found in Frost (2024).

TABLE 3 Cos² values on the first three principal components (PCs) of 17 morphological measurements for female and male *Fejervarya cancrivora*, *F. iskandari* and *F. verruculosa* (left) and *Fejervarya verruculosa* (right) separated by major island clades. Higher cos² value indicates variables with high contribution to observed variance.

Morphological character	*F. cancrivora* + *F. iskandari* + *F. verruculosa*						*F. verruculosa* only					
	Females			Males			Females			Males		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
SVL	0.040	0.688	0.027	0.234	0.338	0.101	0.4071	0.3952	0.0193	0.2728	0.1833	0.323
rHL	0.295	0.215	0.011	0.402	0.008	0.268	0.1674	0.2805	0.4176	0.5837	0.2054	0.0066
rHW	0.445	0.079	0.047	0.359	0.078	0.270	0.5081	0.0377	0.1347	0.0316	0.2588	0.3413
rSTL	0.492	0.116	0.140	0.773	0.010	0.014	0.5426	0.3607	0.0339	0.7029	0.0731	0.1303
rIOD	0.444	0.003	0.013	0.233	0.249	0.068	0.5071	0.0056	0.0566	0.4205	0.0186	0.0977
rEYD	0.199	0.036	0.433	0.343	0.300	0.002	0.2279	0.1459	0.0224	0.0797	0.5143	0.0058
rIND	0.178	0.552	0.012	0.405	0.058	<0.001	0.3909	0.1437	0.1417	0.3853	0.0199	0.1196
rTED	0.136	0.228	0.002	0.133	0.474	0.036	0.0214	0.0135	0.0144	0.049	0.6219	0.0465
rTYD	0.045	0.024	0.559	0.362	0.160	0.065	0.0149	0.3599	0.2072	0.0272	0.0064	0.6257
rUAL	0.572	0.002	0.006	0.407	0.007	0.356	0.5732	0.2026	0.1924	0.2425	0.165	0.1558
rFAL	0.656	0.007	0.021	0.327	0.267	<0.001	0.5928	0.0958	0.0515	0.1584	0.4608	0.0256
rFLL	0.729	0.004	0.014	0.596	0.077	0.146	0.6724	0.055	0.1389	0.4891	0.0574	0.1814
rHAL	0.470	0.110	<0.001	0.081	0.001	0.354	0.7574	0.003	0.0454	<0.001	0.0516	0.6036
rTHL	0.511	0.088	0.094	0.248	0.090	0.135	0.5746	0.0776	0.1087	0.0011	0.5335	0.064
rTIL	0.695	0.004	0.076	0.846	<0.001	<0.001	0.5946	0.1314	0.0773	0.8998	0.0355	0.0096
rHLL	0.724	0.045	0.105	0.741	0.033	0.049	0.6919	0.1153	0.1135	0.5444	0.3231	0.0061
rTFOL	0.541	0.018	0.011	0.580	0.130	<0.001	0.566	0.0268	0.0498	0.5757	0.0247	0.0951
Eigenvalue	7.168	2.268	1.568	7.073	2.279	1.864	7.8104	2.2683	1.8243	5.4643	3.5531	2.8377
Percentage of variance	42.167	13.340	9.225	41.608	13.408	10.967	45.9436	13.3428	10.7311	32.143	20.9007	16.693
Cumulative proportion	**42.167**	**55.570**	**64.732**	**41.608**	**55.106**	**65.892**	**45.9436**	**59.2863**	**70.0175**	**32.143**	**53.0437**	**69.736**

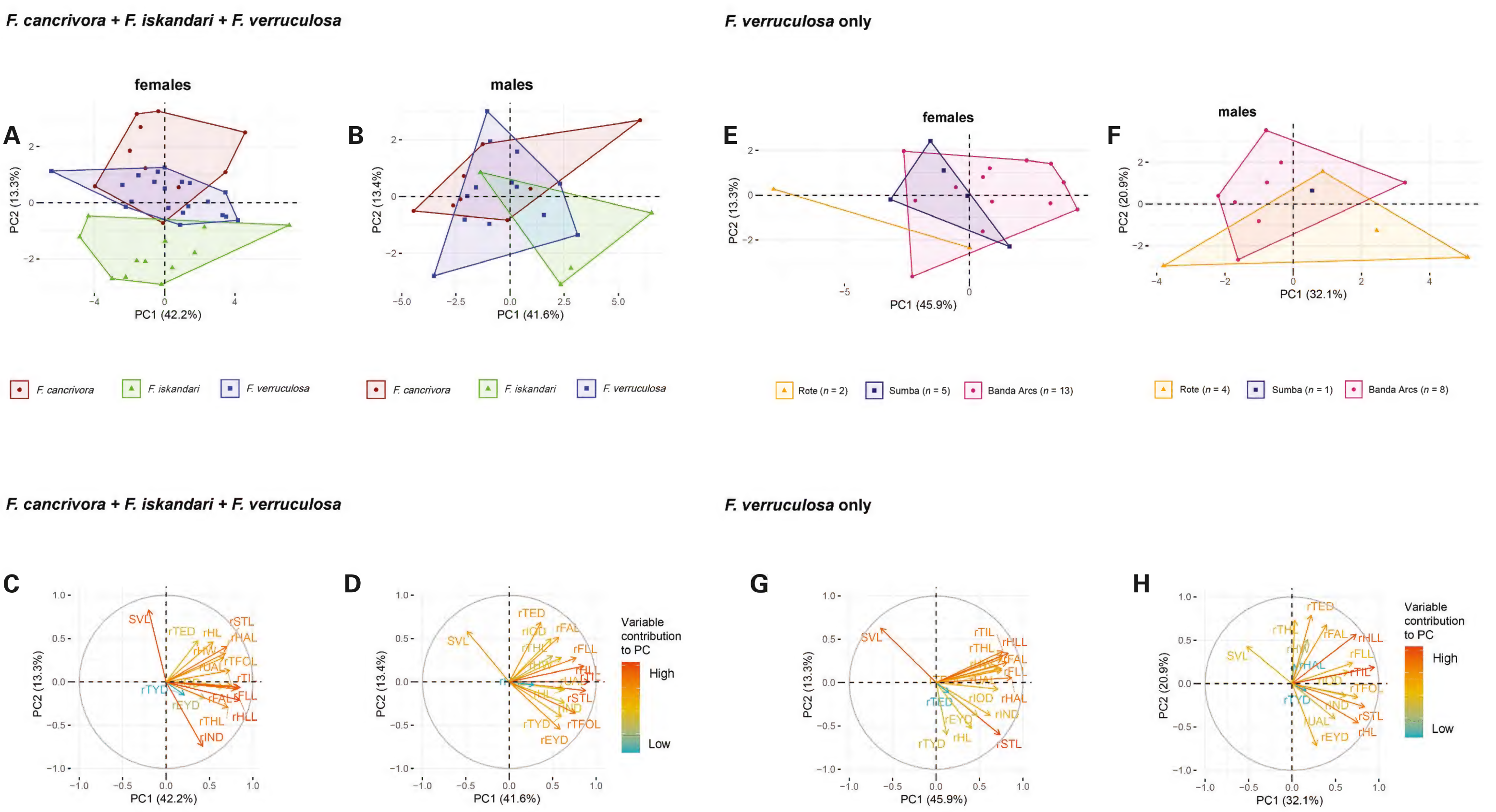

FIGURE 6 Left: Principal components plots (A, B) and correlation circles (C, D) between the first two PCs against morphological measurements from female (A, C) and male (B, D) *Fejervarya cancrivora*, *F. iskandari*, and *F. verruculosa*. Right: Principal components plots (E, F) and correlation circles (G, H) between the first two PCs against morphological measurements from female (E, G) and male (F, H) *Fejervarya verruculosa*, separated by major island clades. See main text for measured values. See main text for measured values.

TABLE 4 Summary of mensural data for examined WAM *Fejervarya cancrivora*, *F. iskandari*, and *F. verruculosa*. Values are means ± SD, followed by range in parentheses. SVL values in mm, all other values standardised as ratio against SVL. *indicates statistical significance from Kruskal-Wallis test.

Morphological character	Females (n = 42)					Males (n = 25)				
	F. cancrivora (♀ = 10)	*F. iskandari* (♀ = 12)	*F. verruculosa* (♀ = 20)	x^2	p-value	*F. cancrivora* (♂ = 8)	*F. iskandari* (♂ = 4)	*F. verruculosa* (♂ = 13)	x^2	p-value
SVL	73.2 ± 13.6 (59–94)	46.4 ± 2.8 (42–51)	60.6 ± 6.8 (50–75)	28.6	<0.01*	60.2 ± 3.8 (56–66)	37.3 ±7.9 (31–49)	48.9 ± 5.3 (39–56)	17.2	<0.01*
rHL	0.23 ± 0.04 (0.20–0.33)	0.20 ± 0.03 (0.16–0.25)	0.21 ± 0.02 (0.19–0.25)	5.2	0.07	0.23 ± 0.02 (0.20–0.27)	0.22 ± 0.02 (0.20–0.24)	0.22 ± 0.03 (0.19–0.28)	1.9	0.40
rHW	0.34 ± 0.02 (0.32–0.37)	0.32 ± 0.03 (0.28–0.37)	0.34 ± 0.03 (0.29–0.38)	4.3	0.11	0.34 ± 0.02 (0.32–0.39)	0.37 ± 0.03 (0.34–0.41)	0.34 ± 0.02 (0.30–0.38)	4.3	0.12
rSTL	0.33 ± 0.06 (0.29–0.48)	0.33 ± 0.03 (0.28–0.40)	0.35 ± 0.02 (0.31–0.38)	8.6	0.01*	0.37 ± 0.02 (0.33–0.42)	0.38 ± 0.23 (0.35 –0.42)	0.36 ± 0.02 (0.33–0.40)	3.5	0.18
rIOD	0.15 ± 0.01 (0.14–0.17)	0.15 ± 0.01 (0.14–0.17)	0.16 ± 0.01 (0.13–0.19)	2.0	0.37	0.16 ± 0.01 (0.14–0.17)	0.15 ± 0.00 (0.15–0.16)	0.16 ± 0.01 (0.14–0.18)	0.1	0.93
rEYD	0.11 ± 0.02 (0.08–0.13)	0.11 ± 0.01 (0.09–0.14)	0.12 ± 0.01 (0.07–0.15)	1.7	0.43	0.12 ± 0.01 (0.10–0.13)	0.13 ± 0.01 (0.12–0.14)	0.12 ± 0.01 (0.11–0.13)	5.0	0.08
rIND	0.06 ± 0.01 (0.06–0.07)	0.07 ± 0.01 (0.06–0.09)	0.07 ± 0.01 (0.06–0.08)	11.9	<0.01*	0.06 ± 0.01 (0.06–0.07)	0.08 ± 0.01 (0.07–0.10)	0.07 ± 0.01 (0.05–0.08)	5.4	0.06
rTED	0.04 ± 0.01 (0.03–0.05)	0.04 ± 0.01 (0.01–0.06)	0.04 ± 0.01 (0.02–0.06)	6.0	0.05*	0.04 ± 0.01 (0.03–0.06)	0.04 ± 0.00 (0.04–0.05)	0.04 ± 0.01 (0.02–0.06)	0.6	0.74
rTYD	0.08 ± 0.01 (0.07–0.09)	0.08 ± 0.01 (0.06–0.10)	0.08 ± 0.01 (0.06–0.09)	1.2	0.54	0.08 ± 0.01 (0.07–0.09)	0.09 ± 0.01 (0.07–0.10)	0.08 ± 0.01 (0.07–0.09)	2.5	0.28
rUAL	0.23 ± 0.03 (0.19–0.28)	0.23 ± 0.02 (0.19–0.27)	0.23 ± 0.02 (0.20–0.26)	0.0	0.98	0.24 ± 0.02 (0.20–0.27)	0.25 ± 0.02 (0.23–0.27)	0.24 ± 0.02 (0.21–0.26)	1.1	0.59
rFAL	0.22 ± 0.02 (0.19–0.25)	0.22 ± 0.02 (0.19–0.25)	0.23 ± 0.02 (0.20–0.26)	2.7	0.26	0.23 ± 0.02 (0.20–0.28)	0.23 ± 0.02 (0.22–0.26)	0.23 ± 0.02 (0.17–0.25)	0.5	0.79
rFLL	0.45 ± 0.04 (0.40–0.53)	0.45 ± 0.04 (0.38–0.52)	0.44 ± 0.04 (0.39–0.51)	0.8	0.65	0.47 ± 0.04 (0.40–0.52)	0.48 ± 0.03 (0.46–0.53)	0.47 ± 0.03 (0.42–0.50)	0.2	0.90

Morphological character	Females (n = 42) F. cancrivora (♀ = 10)	F. iskandari (♀ = 12)	F. verruculosa (♀ = 20)	x^2	p-value	Males (n = 25) F. cancrivora (♂ = 8)	F. iskandari (♂ = 4)	F. verruculosa (♂ = 13)	x^2	p-value
rHAL	0.22 ± 0.02 (0.19–0.24)	0.19 ± 0.02 (0.17–0.26)	0.22 ± 0.02 (0.19 ± 0.44)	11.6	<0.01*	0.23 ± 0.02 (0.20–0.28)	0.24 ± 0.02 (0.21–0.26)	0.23 ± 0.07 (0.19–0.44)	4.4	0.11
rTHL	0.43 ± 0.04 (0.35–0.47)	0.45 ± 0.05 (0.34–0.52)	0.45 ± 0.05 (0.31–0.53)	3.1	0.22	0.42 ± 0.05 (0.36–0.52)	0.45 ± 0.04 (0.40–0.48)	0.45 ± 0.02 (0.40–0.48)	5.5	0.07
rTIL	0.49 ± 0.04 (0.39–0.53)	0.51 ± 0.05 (0.43–0.61)	0.49 ± 0.03 (0.42–0.55)	0.8	0.66	0.49 ± 0.04 (0.44–0.57)	0.53 ± 0.05 (0.46–0.57)	0.48 ± 0.03 (0.44–0.53)	2.6	0.27
rHLL	0.91 ± 0.08 (0.74–1.02)	0.96 ± 0.09 (0.80–1.13)	0.94 ± 0.08 (0.73–1.08)	2.1	0.36	0.91 ± 0.09 (0.80–1.09)	0.98 ± 0.07 (0.92–1.05)	0.94 ± 0.04 (0.87–0.99)	3.7	0.16
rTFOL	0.74 ± 0.04 (0.68–0.80)	0.71 ± 0.07 (0.62–0.84)	0.71 ± 0.07 (0.55–0.81)	1.31	0.52	0.73 ± 0.07 (0.67–0.89)	0.82 ± 0.12 (0.66–0.95)	0.73 ± 0.05 (0.62–0.84)	2.1	0.34
rHL/rHW	0.67 ± 0.11 (0.60–0.97)	0.63 ± 0.10 (0.51–0.79)	0.62 ± 0.08 (0.49–0.86)	1.5	0.47	0.65 ± 0.04 (0.57–0.70)	0.60 ± 0.06 (0.55–0.68)	0.65 ± 0.10 (0.51–0.87)	2.0	0.37
rIOD/rHW	0.45 ± 0.02 (0.41–0.47)	0.48 ± 0.04 (0.39–0.54)	0.46 ± 0.03 (0.41–0.51)	4.6	0.10	0.46 ± 0.02 (0.43–0.51)	0.42 ± 0.03 (0.38–0.46)	0.47 ± 0.04 (0.42–0.54)	4.5	0.10
rTYD/rEYD	0.72 ± 0.08 (0.60–0.81)	0.67 ± 0.07 (0.53–0.82)	0.67 ± 0.12 (0.47–0.97)	4.4	0.11	0.73 ± 0.06 (0.67–0.86)	0.71 ± 0.07 (0.63–0.77)	0.68 ± 0.06 (0.57–0.80)	2.5	0.29
rTED/rEYD	0.40 ± 0.14 (0.22–0.65)	0.32 ± 0.09 (0.13–0.45)	0.41 ± 0.09 (0.29–0.68)	5.1	0.08	0.37 ± 0.09 (0.24–0.50)	0.34 ± 0.04 (0.30–0.38)	0.36 ± 0.10 (0.21–0.54)	0.3	0.88
rFLL/rHLL	0.49 ± 0.05 (0.42–0.57)	0.47 ± 0.02 (0.13–0.45)	0.49 ± 0.04 (0.42–0.55)	4.3	0.12	0.51 ± 0.04 (0.44–0.60)	0.49 ± 0.03 (0.45–0.52)	0.50 ± 0.02 (0.46–0.53)	1.5	0.48
rUAL/rFAL	1.06 ± 0.02 (0.86–1.20)	1.05 ± 0.07 (0.92–1.19)	1.02 ± 0.07 (0.93–1.15)	2.3	0.31	1.03 ± 0.05 (0.96–1.13)	1.06 ± 0.05 (1.03–1.13)	1.04 ± 0.16 (0.87–1.45)	1.0	0.59
rHAL/rFAL	1.01 ± 0.08 (0.91–1.22)	0.89 ± 0.10 (0.71–1.04)	0.95 ± 0.06 (0.86–1.07)	7.8	0.02*	1.00 ± 0.10 (0.82–1.13)	1.02 ± 0.09 (0.93–1.14)	0.99 ± 0.30 (0.75–1.88)	2.8	0.24
rTHL/rTIL	0.87 ± 0.07 (0.77–0.97)	0.90 ± 0.09 (0.70–1.04)	0.91 ± 0.08 (0.75–1.03)	1.8	0.41	0.86 ± 0.07 (0.73–0.92)	0.86 ± 0.11 (0.77–1.02)	0.94 ± 0.07 (0.85–1.04)	5.3	0.07
rTFOL/rTIL	1.51 ± 0.10 (1.34–1.75)	1.40 ± 0.10 (1.27–1.55)	1.45 ± 0.10 (1.15–1.60)	5.6	0.05*	1.51 ± 0.12 (1.32–1.73)	1.55 ± 0.19 (1.43–1.83)	1.51 ± 0.08 (1.30–1.61)	0.5	0.80

Fejervarya cancrivora (Gravenhorst, 1829)

Crab-eating Frog

Figures 7–8

MATERIAL EXAMINED

Specimens collected from Lombok (WAM R98345), Mojo (R98691), Sumbawa (R98416, R98397, R98611, R98616, R98533, R99843), Bali (R109000, R109002, R109003), and Nusa Penida (R109193) (see Appendix 1 for collection details).

Neotype

Indonesia: ***West Java***: FMNH 256688 (Field Museum of Natural History, Chicago, USA) from Cianjur. Designated by Dubois & Ohler (2000).

DIAGNOSIS

A species of the genus *Fejervarya* (sensu Sanchez et al. 2018) identified by the following characters: maximum male SVL 66 mm; maximum female SVL 94 mm; head large, mean rHL 0.23, mean rHW 0.34; tympanum-eye distance short, mean rTED = 0.04; dorsal furrows continuous, interspersed with raised oblong patches extending to the flanks; forelimbs moderately robust, mean rFLL 0.45 in females and 0.47 in males; mean rHAL 0.22 in females and 0.23 in males; hindlimbs robust; tibia slightly longer than thigh; tarsus and foot longer than hindlimb, mean rHLL 0.91; mean rTFOL 0.74 in females and 0.73 in males; dermal fringe on postaxial side of Toe V variably expressed, from absent to well-developed (Figure 8C); inner metatarsal tubercle prominent and elongate, outer metatarsal tubercle absent; foot webbing formula I (1–1.25) II (1–1) III (1–2) IV (2–1) V.

Fejervarya cancrivora differs from Lesser Sundas congeners as follows: from *F. verruculosa* by its larger size (SVL 39–75 mm in *F. verruculosa*), dorsum rugosity (furrows broken into small oblong patches in *F. verruculosa*), a relatively longer head (rHL/rHW 0.23 in *F. cancrivora*; 0.21 in female *F. verrruculosa*, 0.22 in males) and degree of fringing in the post-axial side of Toe V (reduced to a ridge in *F. verruculosa*); from *F. iskandari* by larger size (SVL 31–51 mm in *F. iskandari*), absence of an outer metatarsal tubercle, a relatively longer head (rHL/rHW 0.20 in female *F. iskandari*, 0.22 in males) and longer forelimbs relative to hindlimbs (rFLL/rHLL = 0.49 in female *F. cancrivora*, 0.51 in males versus 0.47 in female *F. iskandari*, 0.49 in males).

DESCRIPTION

Male SVL 47–66 mm; female SVL 59–94 mm. Dorsum slightly rugose with scattered long furrows forming irregular longitudinal rows (Figure 8D). Ventral surface smooth. Head long and wide; side profile acute. Nares semi-ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length; distinct fold present at anterior edge of eye. Tympanum circular with raised annulus. Supratympanic fold emanates from posterior edge of eye and extends posteriorly to axillary region, terminating before shoulder. Upper arm, forearm and hands approximately same relative lengths. Hands approximately same length as lower arm. Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles elongate. Relative finger lengths I < II < IV < III. Prepollax present on Finger I, indistinct. Palmar tubercles circular on Finger II, ovoid on Fingers III + IV. Thighs well-developed and slightly shorter than tibia. Combined tarsus and foot length shorter than combined thigh and tibia length. Toes long, thin, with moderate webbing deeply excised between digits. Relative toe length I < II < V < III < IV. Subarticular tubercles elongate. Toe I webbed to midpoint of distal phalanx; webbing of pre-axial side of Toe II extends slightly beyond distal phalanx; continuing as narrow fringe to tip of digit. Post-axial side of Toe II fully webbed. Pre-axial side of Toe III webbed to distal point of distal subarticular tubercle. Post-axial side of Toe III fully webbed. Webbing on pre-axial and post-axial sides of Toe IV ends at second distal-most subarticular tubercle, where it narrows to lateral fringe which often wraps distal-most parts of digit. Toe V webbed to distal subarticular tubercle, extending as lateral fringe to end of digit. Dermal flap originates from post-axial side of Toe V, wraps around post-axial side of sole, and terminates at base of foot. Inner metatarsal tubercle prominent, elongated; outer metatarsal tubercle absent. Tarsal tubercles and supernumerary tubercles absent.

FIGURE 7 *Fejervarya cancrivora*, Sumbawa, Indonesia (Photo: Ron Johnstone).

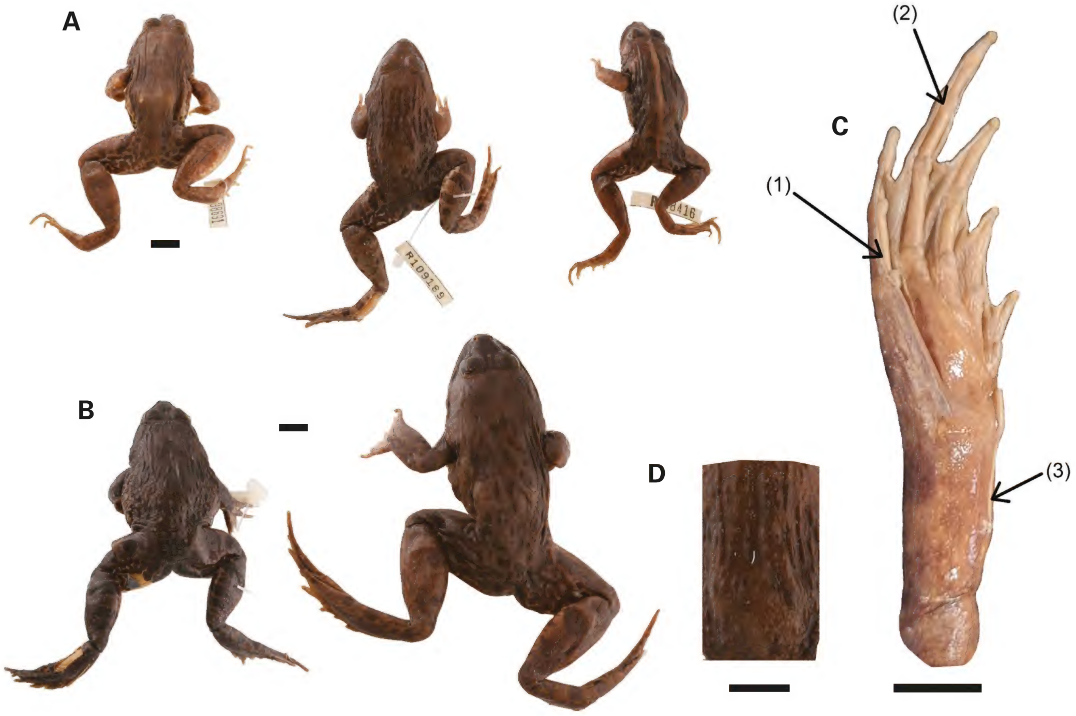

FIGURE 8 Preserved specimens of *Fejervarya cancrivora*. A) males (WAM R98691, R109189, R98416); B) females (WAM R109185, R109000); C) hindlimb (WAM R109189), arrows indicate: (1) post-axial dermal fringe (2), lateral fringing wedded to Toe IV, and (3) inner metatarsal ridge; D) dorsum rugosity (WAM R109000). Scale bars = 10 mm.

Colouration (in preservative)

Dorsum dark brown with darker brown pigmented blotches tending to occur with irregular longitudinal furrows. Ventrum off-white. Sides heavily stippled with dark pigment. Labial region light brown, interspersed with wide dark brown bars extending to lower jaw margin. Forearms covered with dark brown blotches forming loose longitudinal rows. Inside of thigh marbled, pale brown on dark brown. Thighs and tibia covered with transverse rows of round dark brown ovoid spots.

Variation

Females markedly larger than males. Sexually mature males with large, paired triangular blotches on posterior side of each lower jaw, absent in females. Some individuals (2 of 19 examined) with vertebral stripe. Ventral surface of mandible variably stippled with dark brown reticulations. Dermal flap on post-axial side of Toe V variably expressed, with the monophyletic Nusa Penida and Sumbawa populations possessing the flap, whereas it is absent in other populations.

DISTRIBUTION AND ECOLOGY

Fejervarya cancrivora is found in Taiwan, the Malay Peninsula, Sumatra, Java, the Lesser Sunda Archipelago, and is introduced to Guam (Wostl et al. 2016). Its distribution in the Lesser Sundas includes Bali, Nusa Penida, Sumbawa and Mojo Islands (Figure 2A,C), but it does not occur in the Banda Arcs. *Fejervarya cancrivora* is known to inhabit rice paddies and human settlements. It is consumed as a food throughout its range (Kusrini 2005) and one of the primary species exported to European food markets, notably to France (Ohler and Nicolas 2017).

Fejervarya verruculosa **(Roux, 1911)**

Banda Arc Wart Frog

Figure 9

MATERIAL EXAMINED

Specimens collected from Sumba (WAM R101763, R101805, R101681, R101682, R101589, R101593), Rote (R105671, R105681, R105684, R105604, R105611,

R105606, R105600), Semau (R105000, R105876, R105878), Timor (R101508, R101511, R101535, R107045, R107024, R107027, R107035, R107040, R106470, R106651, R106884, R106836, R106855), and Alor (R107785, R107787, R107987) (see Appendix 1 for collection details).

Lectotype

Indonesia: ***Maluku***: SMF 6538 (Naturmuseum Senckenberg. Frankfurt, Germany) from Ilwaki, Wetar Island. Designated by Mertens (1967).

DIAGNOSIS

A species of genus *Fejervarya* identified by the following characters: maximum male SVL 56 mm; maximum female SVL 75 mm; head large, rHL 0.21 in females and 0.22 in males; rHW 0.34; tympanum-ear distance short, rTED 0.04–0.05; dorsal furrows broken into raised oblong patches covering the dorsal surface and flanks; forelimbs moderately robust, rFLL 0.44 in females, 0.47 in males; rHAL 0.22 in females 0.23 in males; hindlimbs robust, tibia longer than thigh; tarsus and foot longer than both thigh and tibia, rHLL 0.94; rTFOL 0.71 in females, 0.73 in males; dermal ridge on the postaxial side of Toe V poorly developed, if present; inner metatarsal tubercle prominent and elongate, outer metatarsal tubercle absent; foot webbing formula I (1–1.25) II (1–1) III (1–2) IV (2–1) V.

Fejervarya verruculosa differs from Lesser Sundas congeners as follows: from *F. cancrivora* by smaller size (SVL 47–94 mm in *F. cancrivora*), dorsum furrows arranged in longer ridges in *F. cancrivora*, degree of fringing in the post-axial side of Toe V (reduced to a ridge; Figure 9C), shorter head (rHL 0.23 in *F. cancrivora*), shorter thighs (rTHL 0.45 in *F. verruculosa,* 0.42 in female *F. cancrivora*, 0.43 in males); from *F. iskandari* by larger size (SVL 31–51 mm in *F. iskandari*), absence of an outer metatarsal tubercle, longer upper arm relative to lower arm (rUAL/rFAL 1.02 in female *F. verruculosa*, 1.04 in males; 1.05 in female *F. cancrivora*, 1.04 in males) and hindlimbs (rHLL = 0.94 in *F. verruculosa*, 0.96 in female *F. iskandari*, 0.98 in males).

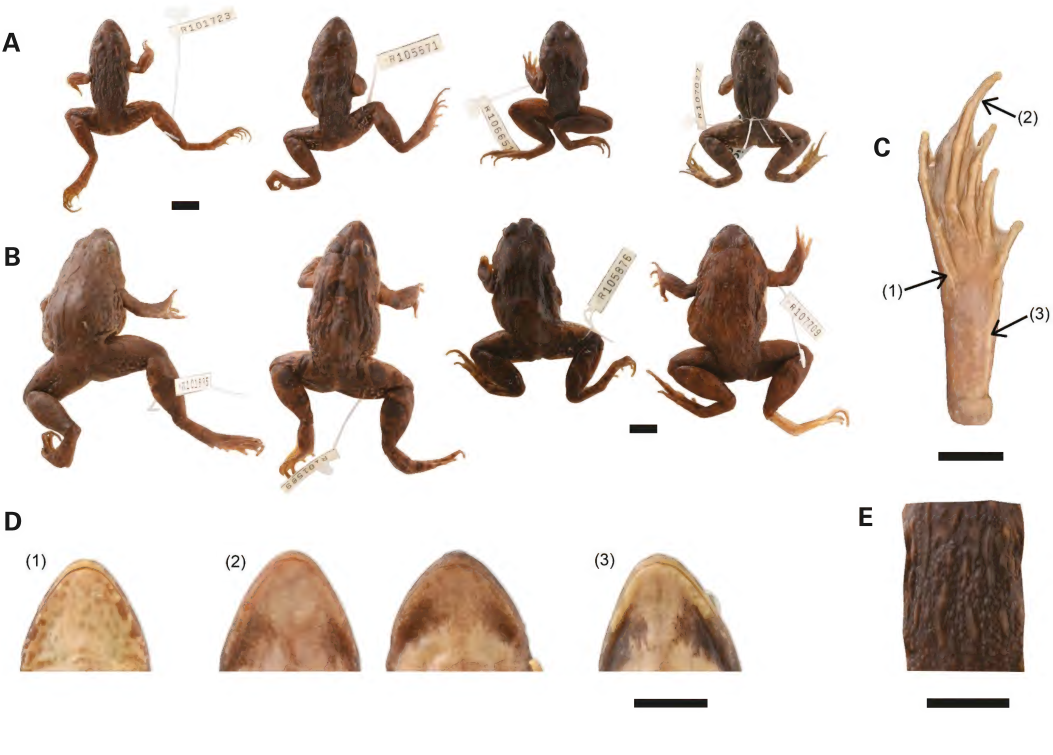

FIGURE 9 Preserved specimens of *Fejervarya verruculosa*. A) males (WAM R101723, R105671, R106651, R107027); B) females (WAM R101535, R101589, R105876, R107709); C) Hindlimb (WAM R101535); arrows indicate: (1) outer toe ridge, (2) distal lateral fringe in Toe IV, and (3) inner metatarsal ridge; D) ontogeny of males: (1) immature (WAM R101723), (2) subadults (WAM R105671, R106651), (3) mature adult (WAM R107027); E) dorsum rugosity (WAM R101723). Scale bars = 10 mm.

DESCRIPTION

Male SVL 39–56 mm; female SVL 50–75 mm. Dorsal furrows broken into raised oblong patches covering dorsal surface and flanks (Figure 9E). Ventral surface smooth. Head long and wide; side profile acute. Nares semi-ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length; distinct fold present at anterior opening of eye. Tympanum circular with raised annulus. Supratympanic fold from posterior edge of eye extending to axillary region, terminating before shoulder. Upper arm longer than the forearm. Hands approximately same length as lower arm. Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles elongated. Relative finger length I < II < IV < III. Prepollax present on Finger I. Palmar tubercles circular on Finger II, oval on Fingers III + IV. Hindlimbs robust. Thighs slightly shorter than tibia. Combined tarsus and foot length shorter than combined thigh and tibia length. Toes long, thin, with moderate webbing not deeply excised between digits. Relative toe length I < II < V < III < IV. Subarticular tubercles elongate. Toe I webbed to the midpoint of the distal phalanx; webbing of pre-axial side of Toe II extends slightly beyond the distal phalanx; continuing as a narrow fringe to digit tip. Post-axial side of Toe II fully webbed. Pre-axial side of Toe III webbed to distal point of distal subarticular tubercle. Post-axial side of Toe III fully webbed. Webbing on pre-axial and post-axial sides of Toe IV ends at second distal-most subarticular tubercle, narrowing to thin fringe on both sides of digit. Toe V webbed to distal subarticular tubercle extending into lateral fringe reaching tip of digit. Dermal ridge originates from proximal subarticular tubercle on post-axial side of Toe V and terminates at post-axial side of the foot. Inner metatarsal tubercle prominent and elongate; outer metatarsal tubercle absent. Tarsal tubercles and supernumerary tubercles absent.

Colouration (in preservative)

Dorsum dark brown with dark pigmented blotches around raised furrows. Ventrum colour variable, ranging from off white to dark brown. Sides lightly stippled with dark brown reticulations. Labial region light brown, interspersed with wide dark brown bars extending to margin of lower jaw. Forearms with dark blotches tending to occur in longitudinal rows. Inside of thigh is marbled, pale brown on dark brown. Thighs and tibia with transverse round dark ovoid spots.

Variation

Females markedly larger than males. Sexually mature males with paired large triangular blotches on posterior side of each lower jaw. Gular coloration ranges from brown to off-white with dark brown stippling present in most individuals. One individual possessed a wide vertebral stripe (of 36 individuals examined).

DISTRIBUTION AND ECOLOGY

Restricted to the Banda Arcs. This species is found on the islands of Rote, Sumba, Pantar, Alor, Timor and Wetar (Figure 2A,C). Unlike its Lesser Sunda congeners, *F. verruculosa* is rarely found near human habitation and appears to be restricted to freshwater rivers and streams.

Fejervarya iskandari
Veith, Kosuch, Ohler & Dubois, 2001

Iskandar's grass frog

Figures 10–11

MATERIAL EXAMINED

Western Australian Museum specimens collected from Sumbawa (WAM R99850, R99849, R99642), Flores (R105393, R105394), and Bali (R109135, R109324, R109313, R109319, R109326, R109317, R109335, R109047, R109066, R109062, R109011) (see Appendix 1 for collection details).

Holotype

Indonesia: ***West Java***: MNHN 1997.4916 (Muséum National d'histoire Naturelle, Paris, France) from Cianjur.

DIAGNOSIS

A small-bodied species of genus *Fejervarya* identified by the following characters: maximum male SVL 49 mm; maximum female SVL 51 mm; head short, rHL 0.20 in females, 0.22 in males; tympanum-ear distance short, rTED 0.04; dorsal furrows continuous, transitioning to raised oblong patches towards the posterior end of the dorsum; forelimbs short, gracile, rFLL 0.45 in females, 0.48 in males; hindlimbs gracile , rHLL 0.96 for females, 0.98 for males; inner metatarsal tubercle prominent and elongate; outer metatarsal tubercle reduced to a small circular knob (Figure 11B); foot webbing formula I (1–2) II (1–2) III (1–3) IV (2.5–1) V.

Fejervarya iskandari differs from both *F. cancrivora* and *F. verruculosa* by its smaller size, reduced sexual size dimorphism, presence of a reduced outer metatarsal tubercle, inner metatarsal line extending slightly diagonally down the tarsus (as opposed to straight in *F. cancrivora* and *F. verruculosa*), longer tibia (rTIL 0.51 in females, 0.53 in males for *iskandari*; ≤ 0.49 in *F. cancrivora* and *F. verruculosa*) and longer hindlimbs (rHLL ≤ 0.94 in *F. cancrivora* and *F. verruculosa*).

DESCRIPTION

Male SVL 31–49 mm; female SVL 42–51 mm. Dorsum with furrows of variable lengths, irregularly arranged anteriorly and transitioning to raised oblong patches posteriorly. Ventral surface smooth. Head small

and wide. Nares ovoid, located closer to snout tip than eye. Eye approximately one-third of total head length. A distinct fold present at anterior edge of eye. Tympanum circular, annulus weakly developed. Supratympanic fold begins at posterior edge of eye extending to axillary region, terminating before shoulder. Forelimbs slender. Forearm longer than upper arm. Hands shorter in females (rHAL 0.19) than males (rHAL 0.24). Fingers stout, unwebbed, terminating in slightly dilated tips. Subarticular tubercles medium and conical. Relative finger length I < II < IV < III. Prominent prepollax present on base of Finger I. Palmar tubercles circular on Finger II and merged to ovoid on Fingers III + IV. Hindlimbs slender. Thighs and tibia gracile; tibia longer than thigh. Tarsus and foot long and thin. Toes long, thin, with moderate webbing not deeply excised between digits. Relative toe length I < II < V < III < IV. Subarticular tubercles small and blade-like. Toe I webbed to the midpoint of the distal subarticular tubercle. Webbing of pre-axial side of Toe II reaches proximal point of distal subarticular tubercle; webbing of post-axial side of Toe II reaches distal point of distal subarticular tubercle. Pre-axial side of Toe III webbed to the distal subarticular tubercle and extends as thin lateral fringe reaching digit terminus (Figure 11B). Post-axial side of Toe III webbed to distal subarticular tubercle. Webbing on pre-axial and post-axial sides of Toe IV ends at third subarticular tubercle from digit terminus, extending to thin fringe merged between second and third subarticular tubercle

FIGURE 10 *Fejervarya iskandari*, Flores, Indonesia (Photos: Sean Reilly).

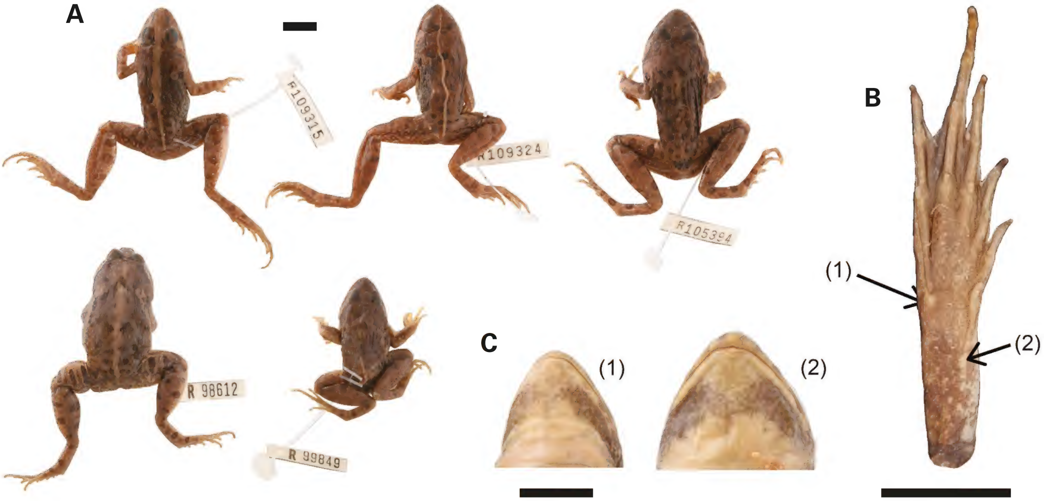

FIGURE 11 Preserved specimens of *Fejervarya iskandari*. A) top row (WAM R109315, R109324 [Bali], R105394 [Flores]), bottom row (WAM R98612; R99849); B) Hindlimb of *F. iskandari* (WAM R109066), arrows indicate: (1) outer metatarsal tubercle, and (2) inner metatarsal ridge; C) ontogeny of males: (1) subadult (WAM R99849); (2) mature adult (R98612). Scale bars = 10 mm.

on both sides of digit. Toe V webbed to the distal subarticulate tubercle extending into a lateral fringe reaching the end of the digit. Dermal ridge present; originates from post-axial side of Toe V terminus and extends to proximal end of basal phalange of Toe V. Inner metatarsal tubercle prominent, elongated; outer metatarsal tubercle reduced to small knob. Dermal line extends from proximal end of inner metatarsal tubercle, extending on angle to base of tarsus. Tarsal tubercles and supernumerary tubercles absent.

Colouration (in preservative)

Light brown dorsum. Dark brown pigmented spots around raised furrows. Ventrum colour off-white. Sides lightly stippled. Bold brown canthal stripe usually present. Labial region light brown, interspersed with narrow dark brown bars extending to margin of lower jaw. Forearms with narrow dark oval blotches tending to form longitudinal rows. Inside of the thigh is marbled, pale brown on dark brown. Thighs and tibia also with narrow dark blotches tending to form longitudinal rows.

Variation

Males and females show overlap in body size. Sexually mature males can be distinguished by: light grey vocal sacs forming an 'M' shape on throat; and patches of fine spines on the throat, prepollax and Finger I. Gular region off-white; light brown gular stippling variably expressed. Individuals exhibit either a wide dorsal vertebral stripe (2 of 12 individuals examined), a thin vertebral stripe with small exterior spots (three individuals) or no vertebral stripe (seven individuals).

DISTRIBUTION AND ECOLOGY

Fejervarya iskandari is endemic to Java, Bali and the Lesser Sundas. In the Lesser Sundas, the range includes the islands of Flores, Sumbawa and Timor (Figure 2B,D). *Fejervarya iskandari* are known to reside around human habitation, but may be found around natural streams as well (Sean Reilly and Jimmy McGuire, pers. obs.).

DISCUSSION

SYSTEMATICS

The natural history and taxonomy of Lesser Sunda *Fejervarya* remain poorly understood for several reasons. Fieldwork in the LS region is challenging owing to costs and logistical coordination, resulting in limited sampling for most islands. This makes the existing specimens available very valuable to understand biogeographic patterns and systematic relationships. The shallow phylogeographic structure and clear pattern of human-mediated dispersal of *F. cancrivora* suggests ongoing gene flow between populations, supporting their current taxonomic status as a single species across the Malay Peninsula and Indonesia. In contrast, mitochondrial DNA data from *F. iskandari* and *F. verruculosa* shows geographic sorting into highly divergent clades. Multi-locus or genomic-level analyses assessing gene flow between mtDNA clades/populations within *F. iskandari* and *F. verruculosa* are required to determine if apparently distinct populations represent separate species despite morphological stasis (unified species concept sensu De Quiroz 2007). Determining the specific status of constituent *F. iskandari* and *F. verruculosa* populations will help to resolve the systematic conundrums of *Fejervarya* and further our understanding of how the unique LS herpetofaunal assemblage formed.

Our study clarifies the phylogenetic position of *Fejervarya verruculosa*, placing it as a sister species to *F. cancrivora* and forming a species complex comprising *F. cancrivora* + *F. verruculosa* + Sulawesi *F.* cf. *cancrivora*. Morphological similarities between *F. cancrivora* and *F. verruculosa* have been noted since their initial description, which is further demonstrated in this study and accurately reflects their close affinity to one another. Early work on *Fejervarya* primarily distinguished *F. verruculosa* from *F. cancrivora* based on the extent of the dermal flap on the post-axial side of Toe V (a 'fringe' in *cancrivora*'; a 'ridge' in *verruculosa*) and furrow lengths on the dorsum (Roux 1911; van Kampen 1923). Interestingly, some *F. cancrivora* individuals lack a prominent dermal fringe on the post-axial side of Toe V entirely. These appear to vary between islands, with some private haplotypes retaining the dermal fringe outside of Toe V (e.g. in Nusa Penida) while others completely lack it (e.g. in Sumbawa). *Fejervarya cancrivora* from west of Wallace's Line exhibit this dermal fringe (van Kampen 1923; Dubois and Ohler 2000; Yodthong et al. 2019a). Understanding patterns of dermal fringe expression between different *F. cancrivora* populations requires more comprehensive morphometric and genomic analyses from both mainland Asian and LS Archipelago.

While our results strongly support the sister relationship between *F. cancrivora* + *F. verruculosa*, vouchers labelled '*F. verruculosa*' have been previously recovered as a sister lineage to *F. iskandari* in mtDNA phylogenies (Köhler et al. 2019; Hasan et al. 2022). We believe that these studies had actually sampled the divergent *F. iskandari* Flores lineage and misattributed them to *F. verruculosa*. This study includes *F. verruculosa* from the type locality of Ilwaki, Wetar Island (Roux 1911) so we are confident in our designation of the *F. verruculosa* and its distribution. Conflicting results in this vein are not unexpected in studies of Indonesian *Fejervarya* (e.g. Djong et al. 2007), highlighting the challenges of species delimitation in this genus.

All three species of *Fejervarya* in the Lesser Sundas and insular populations within *F. iskandari* and *F. verruculosa* show modest to high levels of mtDNA diversity while showing very little morphological

variation between them. Conserved morphologies accompanied by high genetic diversity often occur where allopatric populations assume identical environmental niches, limiting ecological competition and rendering morphological divergence selectively neutral (Pyron et al. 2015; Fišer et al. 2018). Since islands in the LS Archipelago share similar climatic and environmental conditions (Lohman 2011), we hypothesise that this is the likeliest cause for morphological stasis between genetically divergent lineages of Lesser Sunda *Fejervarya*; this has previously been documented in other anurans living in archipelagos (Flury et al. 2021; Ellepolla et al. 2022). Interestingly, patterns of morphological divergence vary in LS herpetofauna. Similar to our *Fejervarya* dataset, some taxa have deeply divergent populations that look nearly identical (e.g. *Sphenomorphus* skinks; Reilly et al. 2022b), while other taxa have very closely related populations which look strikingly different (e.g. emerald tree skinks *Lamprolepis*; Reilly et al. unpublished data).

BIOGEOGRAPHICAL INFERENCES

Interpreting phylogenetic results in a biogeographical context provides an independent line of evidence to understand population divergence and species formation, especially against a backdrop of complex historical biogeography (Arbogast and Kenagy 2001; Fišer et al. 2018) such as in the LS Archipelago. It has been assumed that LS *Fejervarya* frogs are mostly recently introduced due to human activity and therefore less interesting for evolutionary or biogeographic study (Jimmy McGuire, pers. obs.). Here, we present a coarse hypothesis explaining how natural and anthropogenic dispersal of LS *Fejervarya* explain aspects of their contemporary distribution and phylogeographic structures.

The ranges of the three LS *Fejervarya* species roughly correspond to portions of the major tectonic formations in the region, which broadly mirrors the phylogeographic divisions shown in other taxa (Schmitt et al. 2010; Mariyanto et al. 2021). *Fejervarya cancrivora* corresponds to the Sunda Arc, while *F. verruculosa* and *F. iskandari* correspond to the Inner and Outer Banda Arcs, respectively. The shallow phylogenetic structure across Java and the Sunda Arc Islands in *F. cancrivora* is similar to other large-bodied anurans such as *Duttaphrynus melanostictus* and *Polypedates leucomystax*, which was inferred to be a result of human-mediated movement into the LS Archipelago (Brown et al. 2010; Reilly et al. 2017, 2019b). Like *P. leucomystax*, we hypothesise that the lack of phylogenetic structure in LS *F. cancrivora* can be explained by recent human-mediated colonisation in the region, mirroring the spread of agriculture and the movement of *F. cancrivora* as a source of food between communities and islands. Frog meat is consumed in rural areas of Indonesia, and *F. cancrivora* is one of the main species harvested for food (Ohler and Nicolas 2017). Unlike most farmed food sources, *F. cancrivora* are hand-caught adjacent to paddy fields (Kusrini and Alford 2006), presenting a greater chance of individuals escaping into the wild and forming new populations. Alternatively, populations of *F. cancrivora* may have existed in the region but have been highly introgressed with the new colonists, obscuring evidence of phylogeographic structure. The private *F. cancrivora* island haplotypes in Nusa Penida and Sumbawa could have arisen from natural colonisation of those islands, or they could be introduced from populations that are missing in our phylogeny. Presence or absence of gene flow between the haplogroups and introduced populations should be assessed once nuclear genetic data are available for those populations

Fejervarya verruculosa occurs on Sumba and the Banda Arcs. Their phylogenetic position implies that they diverged from naturally dispersing populations of an *F. cancrivora* ancestor moving eastward prior to introgression by human-mediated colonists. Our estimate of the age of the Rote population is enigmatic as this lineage appears much older than the island itself. The common ancestor of *F. verruculosa* diverged from *F. cancrivora* over 6 Ma, even though the islands that *F. verruculosa* occurs on are estimated to be younger than this, especially Rote which is only estimated to have been emergent for ~1 Ma (Roosmawati and Harris 2009). This pattern of old lineages on young islands is well documented, with Christmas Island lizards being a notable example (Oliver et al. 2018; Dodge et al. 2023). Heads (2011) outlined various global examples and possible biogeographic explanations for this pattern. Sumba and Banda Arc Island (minus Rote) clades of *F. verruculosa* are sister to each other, a pattern also found in ranid frogs (Reilly et al. 2022a), *Sphenomorphus* forest skinks (Reilly et al. 2022b), *Draco* flying lizards (Reilly et al. 2022c) and *Cyrtodactylus* bent-toed geckos (Reilly et al. 2023). The divergence estimate of the Sumba lineage is similar to the estimated time at which that island emerged (~3 Ma; Fortuin 1997), and the remaining lineages (Timor, Semau, Alor, Pantar and Wetar) are estimated to be significantly younger than the islands they occupy. The highly nested topology of the tree, with Semau, Alor, Pantar, and Wetar samples nested within Timor samples, suggests that Timor served as the source of dispersal to these neighbouring islands. Pantar and Alor have a shared haplotype suggesting Pantar may have been recently colonised from Alor. As far as we know, *F. verruculosa* is the only known frog species on Pantar Island, which is very hot and dry.

Fejervarya iskandari occurs on the Sunda Arc (Java, Bali, Sumbawa, Flores) and Timor, confirming that their distribution is not restricted to Java. Phylogenetically, *F. iskandari* from Sunda Arc + Timor form a shallow monophyletic clade, like *Polypedates leucomystax*. Timor *F. iskandari* appears to be a recent, human-mediated introduction from Bali and/or Java, which

has also been suggested in *P. leucomystax* (Reilly et al. 2019b). However, the circumstances surrounding the introduction of *F. iskandari* into the Banda Arc remains unclear. Within *F. iskandari*, populations in Sumbawa and Flores naturally diverged from the Sunda Shelf populations approximately 5 Ma, when the archipelago's landscape and geography was significantly different than the present day. Our dataset lacks morphological data from Timor *F. iskandari*, which is worth including in future studies to contextualise this unusual range expansion. Another interesting find is that *F. iskandari* has not yet been confirmed from Lombok though we speculate that *F. iskandari* occurs on the island due to the volume of people and goods moving between Lombok and Bali. However, continued survey efforts are needed to confirm this.

We note that *F. cancrivora* occurs on many of the islands that the dicroglossid frogs of the genus *Limnonectes* occur on, such as Bali, Lombok and Sumbawa. On these islands, *F. cancrivora* is found primarily in rice paddies and human-modified habitats whereas *Limnonectes* occupies more natural mountain streams. In contrast, *F. verruculosa* occurs on islands that do not have any *Limnonectes* frogs, and they tend to be found both in rice paddies and in mountain streams. This suggests that *F. verruculosa* may be occupying a vacant 'stream' niche when *Limnonectes* is absent. The smaller-bodied *F. iskandari* appears to be able to co-occur with larger-bodied *Fejervarya* species, suggesting that they are sufficiently ecologically distinct to limit interspecific competition.

From the combined mitochondrial and morphometric data, we envision a scenario where the common ancestor of both *F. cancrivora* and *F. verruculosa* colonised the Sunda Arc islands of the Lesser Sundas by way of Java, then dispersed out to Sumba and the Banda Arcs where they adopted a stream-living niche and diverged into *F. verruculosa*. Parallel to this, *F. iskandari* colonised the Inner Banda Island arc where they evolved in sympatry with large-bodied dicroglossid frogs in the genus *Limnonectes*.

CONCLUSIONS AND FUTURE DIRECTIONS

We have clarified the phylogenetic relationships of LS *Fejervarya*, placing *F. cancrivora* and *F. verruculosa* as a pair of allopatric sister taxa and confirming the presence of divergent populations of *F. iskandari* in the LS Archipelago. The inclusion of mtDNA topotypes (vouchers from the locality where the type specimen was collected) for all three species allows us to confidently assign vouchers to species, providing updated accounts based on modern systematic techniques and determine the range of all three species with greater precision. While molecular data for *F. cancrivora* indicates a single panmictic population across South-East Asia, data for *F. iskandari* and *F. verruculosa* comprises of several well-diverged populations which roughly corresponds to different LS islands. Gene flow between divergent populations should be assessed to help determine if each clade constitutes a separate species.

A two-pronged hypothesis of dispersal (one by *F. iskandari* and one by *F. cancrivora* + *F. verruculosa*) largely explains the current distribution of Lesser Sundas *Fejervarya*. However, there are several peculiar biogeographical patterns that are difficult to explain. The early diverging *F. verruculosa* lineage on Rote is particularly perplexing. Assuming a direct eastward path from the Sunda Arc into the Banda Arc, this ancestral *Fejervarya* somehow bypassed Sumba through means unknown. The Rote *F. verruculosa* lineage is six times as old as the island itself, indicating this lineage came from somewhere else.

Bioacoustics has been previously applied to delineate *Fejervarya* species (e.g. Köhler et al. 2019), and our study suffered from lack of such calls. It is clear that future studies on Lesser Sunda frogs need to integrate bioacoustics alongside morphological and genomic data. While surveys by WAM, MZB, MVZ and ITB have refined our knowledge of Lesser Sunda *Fejervarya* distributions and diversity, it is likely that more comprehensive surveys will reveal new populations and lineages.

CONTRIBUTIONS

Alen Tanoyo and Sean Reilly jointly drafted the manuscript. Alen Tanoyo measured specimens and performed morphometric analyses. Sean Reilly, Evy Arida, Djoko Iskandar and Jimmy McGuire collected MVZ specimens, Alen Tanoyo and Sean Reilly conducted molecular lab work and analyses. Djoko Iskandar provided systematic and taxonomic clarification, as well as final edits. Paul Doughty and Jimmy McGuire jointly guided experimental design and provided final edits.

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APPENDIX 1 Vouchers of *Fejervarya* analysed in this study. Institutional abbreviations: WAM = Western Australian Museum, Perth, Australia. MVZ = Museum of Vertebrate Zoology, Berkeley, CA, USA. ALS = collected by Alexander Stubbs (Integrative Biology, UC Berkeley).

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R109061	*F. cancrivora*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109065	*F. cancrivora*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109096	*F. cancrivora*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109098	*F. cancrivora*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109000	*F. cancrivora*	Ubud, Bali Island	-8.5000	115.2667		•	•
WAM R109002	*F. cancrivora*	Ubud, Bali Island	-8.5000	115.2667		•	•
WAM R109003	*F. cancrivora*	Ubud, Bali Island	-8.5000	115.2667			•
ALS72	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
ALS73	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274414	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274421	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274422	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274423	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274424	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274425	*F. cancrivora*	Bali Island	-8.4380	115.4020	•		
WAM R109159	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667	•	•	
WAM R109193	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	•
WAM R109149	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109151	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109152	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109154	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109155	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109185	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R109188	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R109189	*F. cancrivora*	Sampalan, Nusa Penida Island	-8.6833	115.5667		•	
WAM R98345	*F. cancrivora*	Kuta, Lombok Island	-8.9166	116.2833		•	•
WAM R98344	*F. cancrivora*	Kuta, Lombok Island	-8.9166	116.2833		•	
MVZ:Herp:293823	*F. cancrivora*	Lombok Island	-8.5320	116.3990	•		
MVZ:Herp:293878	*F. cancrivora*	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp:293879	*F. cancrivora*	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp:293880	*F. cancrivora*	Lombok Island	-8.2690	116.4330	•		
MVZ:Herp:293871	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293872	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293873	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293874	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293875	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293876	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293877	*F. cancrivora*	Lombok Island	-8.5390	116.5400	•		
MVZ:Herp:293900	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293901	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293902	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293903	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293904	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293905	*F. cancrivora*	Sumbawa Island	-9.0280	116.8190	•		
MVZ:Herp:293906	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293907	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293908	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293909	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293910	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293911	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293912	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293913	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293914	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
MVZ:Herp:293915	*F. cancrivora*	Sumbawa Island	-9.0290	116.8190	•		
WAM R98416	*F. cancrivora*	Meraran Lebo, Taliwang, Sumbawa Island	-8.6916	116.8500		•	•
MVZ:Herp:293884	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293885	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293886	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293887	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293888	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:294026	*F. cancrivora*	Sumbawa Island	-8.7580	117.3500	•		
WAM R98475	*F. cancrivora*	Batu Tering, Sumbawa Island	-8.8000	117.3667		•	
MVZ:Herp:293889	*F. cancrivora*	Sumbawa Island	-8.7240	117.3830	•		
WAM R98367	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98374	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5030	117.4333		•	
WAM R98375	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98376	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98377	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98379	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98388	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333		•	
WAM R98387	*F. cancrivora*	Sumbawa Besar, Sumbawa Island	-8.5000	117.4333			•
WAM R98691	*F. cancrivora*	Brang Kua, Mojo Island	-8.2375	117.6125	•	•	•
WAM R98647	*F. cancrivora*	Desa Sebotok, Mojo Island	-8.1583	117.6208		•	
MVZ:Herp:293916	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp:293917	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293918	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp:293919	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp:293920	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp:293921	*F. cancrivora*	Sumbawa Island	-8.3740	118.2840	•		
MVZ:Herp:293824	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293892	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293893	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293894	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293895	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293896	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293897	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293898	*F. cancrivora*	Sumbawa Island	-8.5270	118.3140	•		
MVZ:Herp:293890	*F. cancrivora*	Sumbawa Island	-8.5510	118.3840	•		
MVZ:Herp:293891	*F. cancrivora*	Sumbawa Island	-8.5510	118.3840	•		
WAM R98615	*F. cancrivora*	Desa Daha, Sumbawa Island	-8.7500	118.4333	•	•	
WAM R98611	*F. cancrivora*	Desa Daha, Sumbawa Island	-8.7500	118.4333		•	•
WAM R98616	*F. cancrivora*	Desa Daha, Sumbawa Island	-8.7500	118.4333		•	•
MVZ:Herp:293826	*F. cancrivora*	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp:293923	*F. cancrivora*	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp:293924	*F. cancrivora*	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp:293849	*F. cancrivora*	Sumbawa Island	-8.7660	118.6050	•		
MVZ:Herp:293827	*F. cancrivora*	Sumbawa Island	-8.7400	118.6050	•		
MVZ:Herp:293828	*F. cancrivora*	Sumbawa Island	-8.7400	118.6050	•		
MVZ:Herp:293925	*F. cancrivora*	Sumbawa Island	-8.7630	118.6070	•		
MVZ:Herp:293984	*F. cancrivora*	Sumbawa Island	-8.4870	118.6640	•		
MVZ:Herp:293985	*F. cancrivora*	Sumbawa Island	-8.4870	118.6640	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R98533	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917	•	•	•
WAM R98534	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98535	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98537	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98538	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98539	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R98540	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7917		•	
WAM R99843	*F. cancrivora*	Waworada, Sumbawa Island	-8.7083	118.7920			•
MVZ:Herp:293851	*F. cancrivora*	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp:293852	*F. cancrivora*	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp:293853	*F. cancrivora*	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp:293829	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293830	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293831	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293832	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293833	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293834	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293836	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293838	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293839	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293841	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293842	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293843	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293844	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293845	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293846	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293847	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293848	*F. cancrivora*	Sumbawa Island	-8.5010	119.0360	•		
WAM R109315	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R109324	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	•
WAM R109333	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000	•	•	
WAM R109313	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000		•	•
WAM R109319	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000		•	•
WAM R109320	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000		•	
WAM R109326	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000		•	•
WAM R109317	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000			•
WAM R109335	*F. iskandari*	Gunung Kelatakan, Bali Island	-8.2166	114.5000			•
WAM R109047	*F. iskandari*	Banjar, Bali Island	-8.2000	114.9667	•	•	•
WAM R109066	*F. iskandari*	Banjar, Bali Island	-8.2000	114.9667		•	•
WAM R109048	*F. iskandari*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109064	*F. iskandari*	Banjar, Bali Island	-8.2000	114.9667		•	
WAM R109062	*F. iskandari*	Banjar, Bali Island	-8.2000	114.9667			•
WAM R109011	*F. iskandari*	Ubud, Bali Island	-8.5000	115.2667	•	•	•
MVZ:Herp:274419	*F. iskandari*	Bali Island	-8.4380	115.4020	•		
MVZ:Herp:274420	*F. iskandari*	Bali Island	-8.4380	115.4020	•		
WAM R98397	*F. iskandari*	Merente, 5km SSE Alas, Sumbawa Island	-8.5527	117.0208	•	•	
MVZ:Herp:293881	*F. iskandari*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293882	*F. iskandari*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293883	*F. iskandari*	Sumbawa Island	-8.7580	117.3500	•		
MVZ:Herp:293899	*F. iskandari*	Sumbawa Island	-8.5270	118.3140	•		
WAM R99850	*F. iskandari*	Desa Daha, Sumbawa Island	-8.7500	118.4333			•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R99849	*F. iskandari*	Desa Daha, Sumbawa Island	-8.7500	118.4333			•
WAM R98612	*F. iskandari*	Desa Daha, Sumbawa Island	-8.7500	118.4333			•
MVZ:Herp:293922	*F. iskandari*	Sumbawa Island	-8.4930	118.4920	•		
MVZ:Herp:293850	*F. iskandari*	Sumbawa Island	-8.4850	119.0310	•		
MVZ:Herp:293835	*F. iskandari*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293837	*F. iskandari*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293840	*F. iskandari*	Sumbawa Island	-8.5010	119.0360	•		
MVZ:Herp:293856	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293857	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293858	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293859	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293860	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293861	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293862	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293863	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293864	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293865	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293866	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293867	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293868	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293869	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293870	*F. iskandari*	Flores Island	-8.7230	121.7510	•		
MVZ:Herp:293854	*F. iskandari*	Flores Island	-8.7060	121.7730	•		
MVZ:Herp:293855	*F. iskandari*	Flores Island	-8.7060	121.7730	•		
WAM R105393	*F. iskandari*	Daraloeng Boru, Flores Island	-8.5500	122.6500	•	•	•
WAM R105394	*F. iskandari*	Daraloeng Boru, Flores Island	-8.5500	122.6500	•	•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293819	*F. iskandari*	Flores Island	-8.2160	122.9730	•		
MVZ:Herp:293820	*F. iskandari*	Flores Island	-8.2160	122.9730	•		
MVZ:Herp:293821	*F. iskandari*	Flores Island	-8.2160	122.9730	•		
MVZ:Herp:293822	*F. iskandari*	Flores Island	-8.2160	122.9730	•		
MVZ:Herp:293960	*F. iskandari*	Timor Island	-10.2440	123.6580	•		
MVZ:Herp:293999	*F. iskandari*	Timor Island	-10.0290	123.8620	•		
MVZ:Herp:294000	*F. iskandari*	Timor Island	-10.0290	123.8620	•		
MVZ:Herp:294001	*F. iskandari*	Timor Island	-10.0280	123.8620	•		
MVZ:Herp:294002	*F. iskandari*	Timor Island	-10.0280	123.8620	•		
MVZ:Herp:293990	*F. iskandari*	Timor Island	-10.0240	123.8660	•		
MVZ:Herp:293986	*F. iskandari*	Timor Island	-10.0220	123.8670	•		
MVZ:Herp:293987	*F. iskandari*	Timor Island	-10.0220	123.8670	•		
MVZ:Herp:293988	*F. iskandari*	Timor Island	-10.0220	123.8670	•		
MVZ:Herp:293989	*F. iskandari*	Timor Island	-10.0220	123.8670	•		
MVZ:Herp:293996	*F. iskandari*	Timor Island	-10.0240	123.8680	•		
MVZ:Herp:293997	*F. iskandari*	Timor Island	-10.0240	123.8680	•		
MVZ:Herp:293998	*F. iskandari*	Timor Island	-10.0240	123.8680	•		
MVZ:Herp:293991	*F. iskandari*	Timor Island	-10.0220	123.8690	•		
MVZ:Herp:293992	*F. iskandari*	Timor Island	-10.0220	123.8690	•		
MVZ:Herp:293993	*F. iskandari*	Timor Island	-10.0220	123.8690	•		
MVZ:Herp:293995	*F. iskandari*	Timor Island	-10.0220	123.8690	•		
MVZ:Herp:294003	*F. iskandari*	Timor Island	-10.0240	123.8690	•		
MVZ:Herp:294005	*F. iskandari*	Timor Island	-10.0390	123.9320	•		
MVZ:Herp:294006	*F. iskandari*	Timor Island	-10.0390	123.9320	•		
MVZ:Herp:293962	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293963	*F. iskandari*	Timor Island	-9.8220	124.3100	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293964	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293965	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293967	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293968	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293969	*F. iskandari*	Timor Island	-9.8220	124.3100	•		
WAM R101763	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	•
WAM R101723	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R101765	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500	•	•	
WAM R101721	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500		•	
WAM R101764	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500		•	
WAM R101766	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500		•	
WAM R101805	*F. verruculosa*	Waeelonda, Sumba Island	-9.4333	119.3500			•
WAM R101681	*F. verruculosa*	Waikelosawah, Sumba Island	-9.6000	119.4833		•	•
WAM R101682	*F. verruculosa*	Waikelosawah, Sumba Island	-9.6000	119.4833		•	•
WAM R101685	*F. verruculosa*	Waikelosawah, Sumba Island	-9.6000	119.4833		•	
WAM R101686	*F. verruculosa*	Waikelosawah, Sumba Island	-9.6000	119.4833		•	
MVZ:Herp:293947	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293948	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293949	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293950	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293951	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293952	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293953	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293954	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293955	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293956	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293957	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
MVZ:Herp:293958	*F. verruculosa*	Sumba Island	-10.0070	120.0450	•		
WAM R101580	*F. verruculosa*	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R101581	*F. verruculosa*	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R101582	*F. verruculosa*	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R101584	*F. verruculosa*	Kampong Baru, 2km W Waingapu, Sumba Island	-9.6166	120.2333		•	
WAM R101589	*F. verruculosa*	Waingapu, Sumba Island	-9.6500	120.2500	•	•	•
WAM R101594	*F. verruculosa*	Waingapu, Sumba Island	-9.6500	120.2500	•	•	
WAM R101593	*F. verruculosa*	Waingapu, Sumba Island	-9.6500	120.2500		•	•
WAM R101592	*F. verruculosa*	Waingapu, Sumba Island	-9.6500	120.2500		•	
MVZ:Herp:293946	*F. verruculosa*	Sumba Island	-10.0190	120.6590	•		
WAM R101918	*F. verruculosa*	Ngallu, Sumba Island	-10.1083	120.6917		•	
WAM R101919	*F. verruculosa*	Ngallu, Sumba Island	-10.1083	120.6917		•	
MVZ:Herp:293926	*F. verruculosa*	Rote Island	-10.88800	122.8320	•		
MVZ:Herp:293927	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293928	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293929	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293930	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293931	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293932	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293933	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293934	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293935	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293936	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293937	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293938	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293939	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293940	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293941	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293942	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293943	*F. verruculosa*	Rote Island	-10.8880	122.8320	•		
MVZ:Herp:293944	*F. verruculosa*	Rote Island	-10.7450	123.0540	•		
MVZ:Herp:293945	*F. verruculosa*	Rote Island	-10.7450	123.0540	•		
WAM R105671	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R105681	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R105682	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000	•	•	
WAM R105684	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000	•	•	•
WAM R105622	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000	•	•	
WAM R105621	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000		•	
WAM R105623	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000		•	
WAM R105670	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000		•	
WAM R105604	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000			•
WAM R105611	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000			•
WAM R105606	*F. verruculosa*	Baa, Roti Island	-10.7333	123.1000			•
WAM R105000	*F. verruculosa*	Uiasa, Semau Island	-10.1666	123.4667		•	•
WAM R105876	*F. verruculosa*	Desa Uiasa, Semau Island	-10.1666	123.4667		•	•
WAM R105878	*F. verruculosa*	Desa Uiasa, Semau Island	-10.1666	123.4667		•	•
WAM R105001	*F. verruculosa*	Uiasa, Semau Island	-10.1666	123.4667		•	
WAM R105874	*F. verruculosa*	Desa Uiasa, Semau Island	-10.1666	123.4667		•	
WAM R105877	*F. verruculosa*	Desa Uiasa, Semau Island	-10.1666	123.4667		•	
WAM R108085	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R108086	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108087	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108088	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108089	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108122	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108124	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108126	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108128	*F. verruculosa*	Onansila, Semau Island	-10.2166	123.5000		•	
WAM R108175	*F. verruculosa*	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R108176	*F. verruculosa*	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R108177	*F. verruculosa*	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R108178	*F. verruculosa*	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
WAM R108179	*F. verruculosa*	Lifuleo Oisina, West Timor, Timor Island	-10.3000	123.5000		•	
MVZ:Herp:294007	*F. verruculosa*	Timor Island	-10.2660	123.5660	•		
MVZ:Herp:293959	*F. verruculosa*	Timor Island	-10.2440	123.6580	•		
WAM R101508	*F. verruculosa*	Baumata, West Timor, Timor Island	-10.1833	123.7167	•	•	•
WAM R101511	*F. verruculosa*	Baumata, West Timor, Timor Island	-10.1833	123.7167		•	•
WAM R101535	*F. verruculosa*	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	•
WAM R101517	*F. verruculosa*	Baumata, West Timor, Timor Island	-10.1833	123.7167		•	
WAM R101534	*F. verruculosa*	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R101565	*F. verruculosa*	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R101566	*F. verruculosa*	Buraen, West Timor, Timor Island	-10.2500	123.7167		•	
WAM R107045	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667	•	•	•
WAM R107024	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•
WAM R107027	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•
WAM R107035	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R107040	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	•
WAM R107015	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107017	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107020	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107022	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107025	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107028	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107029	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107030	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107032	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107033	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107037	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107041	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107043	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107044	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107047	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107048	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107049	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107050	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107051	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107052	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107053	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107054	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107058	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107059	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107060	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R107062	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107063	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107064	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107065	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107066	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107067	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107068	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107069	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107071	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107072	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
WAM R107073	*F. verruculosa*	Kokabis, West Timor, Timor Island	-10.1833	123.7667		•	
MVZ:Herp:293994	*F. verruculosa*	Timor Island	-10.0220	123.8690	•		
MVZ:Herp:294004	*F. verruculosa*	Timor Island	-10.0390	123.9320	•		
WAM R101567	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R101568	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R101569	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R101570	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R101571	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R101572	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R107213	*F. verruculosa*	Camplong, West Timor, Timor Island	-9.9750	124.0000		•	
WAM R106470	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167	•	•	•
WAM R106651	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167	•	•	•
WAM R106400	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106402	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106403	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106413	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106415	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106637	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106638	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106640	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106641	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106642	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106643	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106645	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106649	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106650	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106654	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106655	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
WAM R106656	*F. verruculosa*	Nenas, West Timor, Timor Island	-9.5500	124.2167		•	
MVZ:Herp:293974	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293975	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293976	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293977	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293978	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293979	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293980	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
MVZ:Herp:293981	*F. verruculosa*	Timor Island	-9.6570	124.2240	•		
WAM R107899	*F. verruculosa*	Kabir, Pantar Island, Alor Archipelago	-8.2166	124.2333		•	•
WAM R106884	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	•
WAM R106885	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106886	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106887	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106888	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106889	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106890	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106892	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106893	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106894	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106895	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106896	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106897	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106898	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106902	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106903	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106904	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106905	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106906	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106907	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106908	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106909	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106911	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106912	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106913	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106914	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106916	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106917	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106918	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106919	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106920	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R106921	*F. verruculosa*	Oimoro, West Timor, Timor Island	-10.1333	124.2833		•	
WAM R107861	*F. verruculosa*	Batu Bakalang, Pantar Island, Alor Archipelago	-8.2333	124.3000		•	
MVZ:Herp:293961	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293966	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293970	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293971	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293972	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
MVZ:Herp:293973	*F. verruculosa*	Timor Island	-9.8220	124.3100	•		
WAM R106836	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833	•	•	•
WAM R106855	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	•
WAM R106787	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106788	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106789	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106790	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106792	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106799	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106801	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106802	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106803	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106811	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106812	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106813	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106814	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106816	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106817	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
WAM R106831	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106832	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106833	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106834	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106835	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106837	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106838	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106846	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106856	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106857	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106861	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106862	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R106863	*F. verruculosa*	Oihala, West Timor, Timor Island	-9.8333	124.4833		•	
WAM R107708	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	•
WAM R107646	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107651	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107786	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333		•	
WAM R107785	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333			•
WAM R107787	*F. verruculosa*	Kalabahi, Alor Island, Alor Archipelago	-8.2333	124.5333			•
MVZ:Herp:293818	*F. verruculosa*	Alor Island	-8.1640	124.6690	•		
WAM R108075	*F. verruculosa*	Apui, Alor Island, Alor Archipelago	-8.2500	124.7167		•	
WAM R107987	*F. verruculosa*	Apui, Alor Island, Alor Archipelago	-8.2500	124.7167			•
MVZ:Herp:293809	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293810	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293811	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293812	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293813	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293814	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293815	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293816	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293817	*F. verruculosa*	Alor Island	-8.2740	124.7220	•		
MVZ:Herp:293776	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293777	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293778	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293779	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293780	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293781	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293782	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293783	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293784	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293785	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293786	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293787	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293788	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293789	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293790	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293791	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293792	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293793	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293794	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293795	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293796	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:293797	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293798	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293799	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293800	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293801	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293802	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293803	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293804	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293805	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293806	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293807	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:293808	*F. verruculosa*	Alor Island	-8.1650	124.7480	•		
MVZ:Herp:294016	*F. verruculosa*	Wetar Island	-7.9220	126.3990	•		
MVZ:Herp:294009	*F. verruculosa*	Wetar Island	-7.9300	126.4090	•		
MVZ:Herp:294017	*F. verruculosa*	Wetar Island	-7.9300	126.4090	•		
MVZ:Herp:294021	*F. verruculosa*	Wetar Island	-7.9290	126.4100	•		
MVZ:Herp:294010	*F. verruculosa*	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp:294011	*F. verruculosa*	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp:294018	*F. verruculosa*	Wetar Island	-7.9370	126.4120	•		
MVZ:Herp:294019	*F. verruculosa*	Wetar Island	-7.9300	126.4120	•		
MVZ:Herp:293982	*F. verruculosa*	Wetar Island	-7.9280	126.4220	•		
MVZ:Herp:294008	*F. verruculosa*	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp:294012	*F. verruculosa*	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp:294013	*F. verruculosa*	Wetar Island	-7.9310	126.4220	•		
MVZ:Herp:294024	*F. verruculosa*	Wetar Island	-7.9290	126.4230	•		
MVZ:Herp:294022	*F. verruculosa*	Wetar Island	-7.9320	126.4230	•		

Voucher	Species	Locality	Latitude (S)	Longitude (E)	mtDNA (16S)	mtDNA (CO1)	Morphological examination
MVZ:Herp:294023	*F. verruculosa*	Wetar Island	-7.9320	126.4230	•		
MVZ:Herp:294025	*F. verruculosa*	Wetar Island	-7.9320	126.4230	•		
MVZ:Herp:294020	*F. verruculosa*	Wetar Island	-7.9290	126.4240	•		
MVZ:Herp:294014	*F. verruculosa*	Wetar Island			•		
MVZ:Herp:294015	*F. verruculosa*	Wetar Island			•		

APPENDIX 2 GenBank 16S sequences used as outgroups. Full references provided in the main text.

Genbank accession	Species	Locality	Reference
AP011543	*Hoplobatrachus tigrinus*	Mymensingh, Bangladesh	Alam et al. (2010)
MH087466	*Fejervarya kawamurai*	Guizhou, China	Cheng et al. (2018)
MN987553	*Fejervarya multistriata*	Sichuan, China	Jiang et al. (2020)
AY158705	*Fejervarya limnocharis*	Yancheng, China	Liu et al. (2005)
NC012647	*Fejervarya cancrivora*	Guangxi, China	Ren et al. (2009)
AB444693	*Fejervarya* cf. *cancrivora* (Sulawesi-type)	Pelabuhan Ratu, Indonesia	Kurniawan et al. (2010); assigned by Kurniawan et al. (2010) and Yodthong et al. (2019)
AB444689	*Fejervarya cancrivora*	Bogor, Indonesia	Kurniawan et al. (2010)
AB444684	*Fejervarya cancrivora*	Cianjur, Indonesia	Kurniawan et al. (2010)
AB444690	*Fejervarya cancrivora*	Banyumas, Indonesia	Kurniawan et al. (2010)
AB444692	*Fejervarya moodiei*	Trat, Thailand	Kurniawan et al. (2010); re-assigned by inference from Yodthong et al. (2019)
AB444691	*Fejervarya moodiei*	Trat, Thailand	Kurniawan et al. (2010); re-assigned by inference from Yodthong et al. (2019)
AB444688	*Fejervarya cancrivora*	Selangor, Malaysia	Kurniawan et al. (2010)

Genbank accession	Species	Locality	Reference
AB444687	*Fejervarya cancrivora*	Jambi, Indonesia	Kurniawan et al. (2010)
AB444686	*Fejervarya cancrivora*	Lampung, Indonesia	Kurniawan et al. (2010)
AB444685	*Fejervarya cancrivora*	Padang, Indonesia	Kurniawan et al. (2010)
MW007342	*Fejervarya* sp. (Borneo-type)	Sarawak, Malaysia	Flury et al. (2021)
KR816720	*Fejervarya cancrivora*	Mangliano, Guam	Wostl et al. (2016)
KR816719	*Fejervarya cancrivora*	Mangliano, Guam	Wostl et al. (2016)
KR816718	*Fejervarya cancrivora*	Agat, Guam	Wostl et al. (2016)
AB488882	*Fejervarya moodiei*	Selangor, Malaysia	Kotaki et al. (2010); re-assigned by inference from Yodthong et al. (2019)
EU979849	*Fejervarya* cf. *cancrivora* (Sulawesi-type)	South Sulawesi, Indonesia	Che et al. (2007); re-assigned by Yodthong et al. (2019)
EU435303	*Fejervarya cancrivora*	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435280	*Fejervarya cancrivora*	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435282	*Fejervarya cancrivora*	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
EU435279	*Fejervarya cancrivora*	Taiwan	Kung, F.C., Hsu, I., and Yang, M.C. (2008), publication status unknown
DQ458252	*Fejervarya moodiei*	Hainan, China	Che et al. (2009); re-assigned by Yodthong et al. (2019b)
AF206473	*Fejervarya moodiei*	Negros Island, Phillipines	Chen et al. (2005); re-assigned by Yodthong et al. (2019)
AB070738	*Fejervarya moodiei*	Manila, Phillipines	Sumida et al. (2002); re-assigned by Yodthong et al. (2019)
KX055955	*Fejervarya cancrivora*	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)
KX055954	*Fejervarya cancrivora*	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)
KX055953	*Fejervarya cancrivora*	Indonesian commercial export, purchased in Paris, France	Ohler and Nicolas (2017)

Genbank accession	Species	Locality	Reference
MK396095	*Fejervarya moodiei*	Hainan, China	Zheng et al. (2021); re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396094	*Fejervarya moodiei*	Guangdong, China	Zheng et al. (2021); re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396093	*Fejervarya moodiei*	Hainan, China	Zheng et al. (2021); re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396092	*Fejervarya moodiei*	Guangdong, China	Zheng et al. (2021); re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
MK396091	*Fejervarya moodiei*	Guangdong, China	Zheng et al. (2021); re-assigned by inference from Yodthong et al. (2019), which was not referenced in the former publication
AB570277	*Fejervarya cancrivora*	Bali, Indonesia	Kurniawan et al. (2014)
AB570276	*Fejervarya cancrivora*	Bali, Indonesia	Kurniawan et al. (2014)
AB570275	*Fejervarya cancrivora*	Bali, Indonesia	Kurniawan et al. (2014)
AB570274	*Fejervarya cancrivora*	Bali, Indonesia	Kurniawan et al. (2014)
AB570273	*Fejervarya cancrivora*	Malang, Indonesia	Kurniawan et al. (2014)
AB570272	*Fejervarya iskandari*	Banyuwangi, Indonesia	Kurniawan et al. (2014)
AB570271	*Fejervarya iskandari*	Malang, Indonesia	Kurniawan et al. (2014)
AB530613	*Fejervarya iskandari*	Cianjur, Indonesia	Hasan et al. (2014)
AB277303	*Fejervarya iskandari*	Cianjur, Indonesia	Kotaki et al. (2008)
AB526324	*Fejervarya iskandari*	Banyuwangi, Indonesia	Matsui et al. (2010)
AB570270	*Fejervarya iskandari*	Malang, Indonesia	Kurniawan et al. (2014)
AB570269	*Fejervarya iskandari*	Malang, Indonesia	Kurniawan et al. (2014)
AB570268	*Fejervarya iskandari*	Malang, Indonesia	Kurniawan et al. (2014)

SHORT COMMUNICATION

Densities of feral honey bee colonies utilising tree hollows in central Perth, Western Australia

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KEYWORDS: Honey bees, *Apis mellifera*, colony, tree hollows, densities

INTRODUCTION

The European honey bee (*Apis mellifera*) has been present in Australia for over a century (Hopkins 1911) and there is now a well-established honey bee industry which generates large revenues and provides jobs for many people across the country (Rodriquez 2003).

One of the many challenges facing apiculturists is the management of swarms (Jacobs et al. 2017). Losing a colony to swarming reduces apiary productivity and releases a feral colony to the landscape. A feral colony is simply one that exists in the absence of management. The term feral applies to any escape livestock that, like these honey bees, persist in the environment without husbandry.

Indeed, feral colonies have been well documented to occur in natural areas (Oldroyd et al. 1994; Oldroyd et al. 1996; Cunningham et al. 2022; Hinson et al. 2015). A major concern is that feral colonies are often not monitored resulting in uncertainty about densities and therefore impacts of feral colonies.

One detrimental impact of feral colonies is that they often occupy spaces which would otherwise be suitable for native Australian wildlife. This has been demonstrated for regent parrots (Oldroyd et al. 1994), sugar gliders (Wood et al. 1998), Carnaby's Cockatoos (Saunders et al. 2014), and Leadbeater's Possums (Lindenmayer et al. 2009). Such findings have led to efforts to provide alternative nest boxes for native wildlife, including using PVC materials instead of timber which are shown to reduce the risk of occupancy by feral honey bees (Berris and Barth 2020). These conservation efforts are promising, however, the lack of monitoring of feral honey bee colonies is alarming considering the already known impacts that the colonies are having on native wildlife.

Additional negative implications of feral honey bee colonies on native biodiversity include increasing the spread of weeds by pollinating their flowers (Goulsen et al 2004; Simplson et al. 2015), floral resource competition with native pollinators (Geslin et al. 2017; Prendergast and Ollerton 2023), and reducing the fecundity of native bees (Paini et al. 2005).

Furthermore, there is an increasing amount of literature on the impacts of honey bees on native bees, some of which indicates negative effects of competition on native bee abundance, reproductive output, and species richness (Prendergast et al. 2023). This is often exaggerated when feral honey bee colonies are considered, as opposed to managed hives, with feral colonies often surviving longer periods of time, being more aggressive, and being more mobile than managed colonies (Prendergast et al. 2023).

More work is needed to pinpoint the precise impacts on native bees with a focus on how competition with honey bees may effect species ecology. However, to leave feral colonies unmonitored, and under-studied, is leaving native biodiversity vulnerable to the impacts, both those already documented and those yet to be discovered.

This short note is to communicate the feral honey bee colonies found during a systematic survey of central Perth and to provide a minimum colony density estimate for the city.

METHODS

The centre of Perth, Western Australia, was surveyed for feral honey bee colonies using tree cavities. A study area of 5.85 km^2 was demarcated which included the Central Business District (CBD), East Perth, and West Perth. The city consists of many high-rise buildings, roads, several pedestrianised streets, and multiple parks. The study area is encompassed by the Swan River to the east and south. To the southwest is Kings Park Botanical Gardens, whilst to the north and west is a mix of high- and low-density buildings.

Publicly accessible roads and parks within the study area boundary (Figure 1) were walked by the researcher in December 2022 and early January 2023.

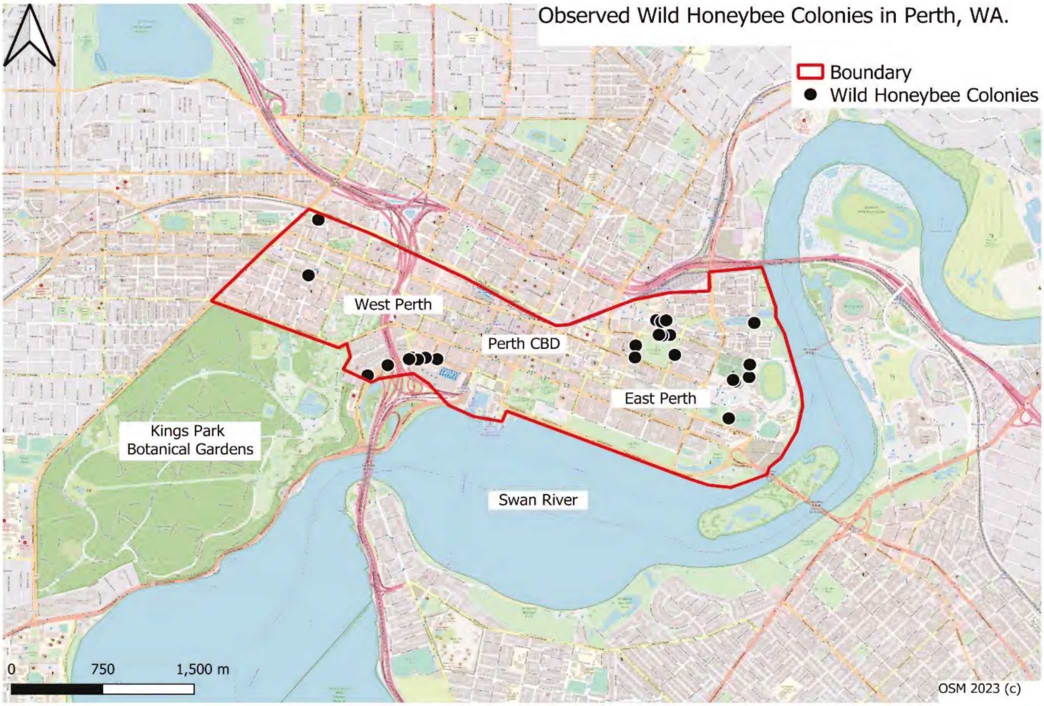

FIGURE 1 Observed feral honey bee colonies in Perth, Western Australia. The figure indicates feral honey bee colonies in tree hollows recorded during this survey with a black circle. The study area is indicated by the bold red boundary within which roads and parks were surveyed.

Each tree found was carefully checked and inspected for scars, cavities, holes, and hollows. If found, these were then observed for up to 30 minutes. The recorder watched until the 30 minutes was expired or if honey bees were observed entering or exiting the hole. Observations were made on warm and sunny days commensurate with honey bee activity.

The locations of each observed feral colony were recorded and categorised as either a park or a street. The categorisation was based on if the tree observed was on a road or if it was within the boundary of a park.

A feral honey bee colony density estimate was calculated by dividing the number of colonies observed by the area surveyed. The area used for this measurement is the area of the parks and roads surveyed. Shapefiles of the road network (Main Roads Western Australia 2024) and parks (City of Perth 2024) were downloaded and used to calculate this area. 602 roads equating to approximately 76.61 km were surveyed and the approximate width of a standard urban two-land road (7.4 m) was used to calculate an area of 0.56 km^2. A total of 24 parks in the study area were surveyed and these measured an area of approximately 0.83 km^2. As such, a total area of approximately 1.39 km^2 was surveyed for feral honey bee colonies using tree hollows.

RESULTS

Twenty-six colonies were found inside the study area at eight different locations (Table 1 and Figure 1). The surveyed area has an estimated density of 18.57 colonies per km^2.

DISCUSSION

I find that feral honey bee colonies exist at a density of 18.57 colonies per km^2 across the surveyed area of central Perth, Western Australia. My findings are higher than existing colony density estimates in the literature for cities. For instance, they sit above the reported density of 6.5 colonies per km^2 in Paris (Ropars et al. 2019). Our study does not include the expansive forested Kings Park Botanical Gardens whereas the study in France did include Bois de Boulogne and Bois de Vincennes. As such, I interpret that my results could be at the higher end of density estimates for a metropolitan city. Furthermore, my findings indicate that the feral honey bee colony densities could be even higher if the study was expanded to the nearby botanical gardens which is extensively forested.

The lack of large woodland areas in our study also helps to explain our lower density estimates when compared to the 50–150 colonies per km^2 recorded in

TABLE 1 Feral Honey bee colonies observed in the central Perth study area, Western Australia.

Location	Category	Colonies
East Perth Cemetery	Park	5
Queens Gardens	Park	1
Totterdell Park	Park	1
Victoria Gardens	Park	2
Wellington Square	Park	6
Hay Street (West Perth)	Street	1
Mounts Bay Road	Street	7
Royal Street	Street	3
Total		**26**

Australian forests (Cunningham et al. 2022; Oldroyd et al. 1997). As such, I consider that the higher number of colonies observed in some of the parks in this study, such as Wellington Square with six colonies and the East Perth Cemetery with five colonies, are likely realistic for areas with more trees, and, likely, a result of more tree cavities being available to be occupied. Furthermore, two streets where I recorded high numbers of feral colonies, Mounts Bay Road with seven colonies and Royal Street with three colonies, were lined with mature tree species, suggesting, that it is the presence of the larger trees, rather than the land categorization, influencing higher densities.

The density reported in this study is concerning for native cavity dwelling species. The feral colonies in these locations are reducing the amount of suitable habitat for native species which has already been demonstrated for birds (Oldroyd et al. 1994; Saunders et al. 2014; Berris and Barth, 2022) and mammals (Wood and Wallis 1998; Lindenmayer et al. 2009).

The presence of the feral colonies is also alarming because of the documented competition with native pollinators for floral resources (Paini and Roberts 2005; Pendergast et al. 2021; Pendergast and Ollerton 2022). The combination of limited native habitat in the city and the competition from feral honey bees may be impacting the already teetering balance our native species must endure to persist.

An important consideration is that the density estimate provided is a minimum estimate for the area considered and that feral honey bee colonies may have been overlooked during this study. For instance, I do not consider feral honey bee colonies in private gardens or on buildings and it is relatively well documented that urban feral honey bee colonies are often found in human made structures such as in residential dwellings and water meter boxes (Baum et al. 2011).

Furthermore, feral colonies can persist high up in trees and whilst every effort was taken to carefully check all the trees, it is possible that small or hidden colonies were not detected. Despite this, our findings highlight the importance of monitoring for feral colonies in our landscapes to better understand their persistence and allow examination of the impacts they may be having on native species.

I highlight the importance of better managing the swarming process to ensure that managed beehives are not releasing swarms into our landscape which already has a density of feral honey bee colonies with the potential to detrimentally impact our native species and habitats. One practical measure to control swarms from managed beehives would be to improve the detection of queen cells (Buttstedt et al. 2018). It is already widely accepted that continuous monitoring for developing queen cells is one of the best methods which allows beekeepers to predict, manage, and mitigate for swarming.

I summarise that central Perth, Western Australia, has a relatively high feral honey bee colony density compared to that of other metropolitan cities and that the few park area and streets with mature trees are supporting high densities. It is crucial to continue monitoring feral colonies to better understand the influences on other species.

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SHORT COMMUNICATION

Range extension of the Whitefin Swellshark *Cephaloscyllium albipinnum* (Scyliorhinidae) and possible implications for its conservation status

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KEYWORDS: Scyliorhinidae, range extension, Albany, IUCN Red List, conservation

INTRODUCTION

Eight species of swellsharks, genus *Cephaloscyllium*, occur in Australian waters, with four occurring in Western Australia. The Reticulate Swellshark *C. hiscosellum* White & Ebert, 2008 and Speckled Swellshark *C. speccum* Last, Séret & White, 2008 are endemic to northern Western Australia. The Whitefin Swellshark *C. albipinnum* Last, White & Motomura, 2008 and Draughtboard Shark *C. laticeps* (Duméril, 1853) have southern Australian distributions including south-eastern Western Australia.

Cephaloscyllium albipinnum is a large swellshark known from southern Australia from Batemans Bay in New South Wales (35°39'S) to off Eucla in the Great Australian Bight, Western Australia, including Tasmania (Figure 1). It is a deeper dwelling species than its sympatric congener *C. laticeps*, occurring at depths of 125–555 m vs. less than 60 m depth in the latter species (Last and Stevens 2009). Off Western Australia, *C. albipinnum* is only known from one adult male (CSIRO CA 3325) collected off Eucla (33°17'S, 128°23'E) in 1981 (Last et al. 2008). Based on its current distribution, *C. albipinnum* has been assessed as Critically Endangered by the IUCN *Red List of Threatened Species* since its entire depth and geographic range has been subjected to intensive trawling as part of the Southern and Eastern Scalefish and Shark Fishery (SESSF) over several decades, which is still ongoing (Pardo et al. 2019). While species-specific data are not available, a population reduction of more than 80% over the past three generations has been inferred (Pardo et al. 2019).

The presence of a swellshark-like egg case collected from off Albany in the fish collection of the Western Australian Museum prompted the authors to investigate whether any swellsharks are observed in fisheries operating in this region.

MATERIALS AND METHODS

The primary author contacted staff at the Department of Primary Industries and Regional Development (DPIRD) in Western Australia to request images of any sharks caught in deep water fisheries off the Albany region. Within several weeks, a fisher supplied images of a large swellshark caught in a commercial giant crab trap at a depth of 260 m (Figure 2). The fisher stated that they are ‘not that rare’ and can get a couple a month in their traps. This fisher is now retired but was previously fishing with an 80-pot license. Following these image records, a request for specimens was made and soon after the authors were notified by DPIRD that they had two frozen swellshark specimens provided by the fisher.

The frozen specimens were taken to the Western Australian Museum and then sent to the Australian National Fish Collection for preservation and subsequent examination. The two specimens were thawed, photographed, tissue (muscle) sample taken, registered, and then fixed in 10% formalin prior to stepping up into 70% ethanol for long-term preservation. The two specimens were compared with the original description of *C. albipinnum* (Last et al. 2008). Subsamples of the muscle sample were submitted

for sequencing of commonly used mitochondrial DNA markers, i.e. cytochrome oxidase subunit 1 (*CO1*) and NADH dehydrogenase subunit 2 (*ND2*), to assist with verifying species identification.

Collection data for the two specimens is as follows: commercial King Crab gear (Southern Rock Lobster pots), south-east of Albany, Western Australia, 35°19.3'S, 118°23.4'E, 260 m depth, collected 6 August 2022 by L. Matthews. One specimen was a 919 mm TL adolescent male, registered as CSIRO H 8957-01; second specimen was a 791 mm TL female, registered as WAM P.35569-001.

RESULTS AND DISCUSSION

The two swellsharks from off Albany agreed well with the type specimens of *C. albipinnum* from southeastern Australia. The characteristic arrangement of dark blotches and saddles on the upper half of the body was consistent with the known colour pattern of *C. albipinnum*. The large size of the adolescent male specimen, i.e. 919 mm TL, is much larger than the size at maturity for males provided for *C. albipinnum* in Last and Stevens (2009), i.e. by 700 mm TL. However, males examined by Last et al. (2008) were still immature at 762 mm TL and the smallest adult male was 895 mm TL. Thus, a size at maturity of between 895 and at least 920 mm TL is likely for this species and the size at maturity of 700 mm TL proposed by Last and Stevens (2009) appears to be an underestimate. The *ND2* and *CO1* sequences also confirmed these specimens as being *C. albipinnum* (G. Naylor, Florida Museum of Natural History; and S. Appleyard, CSIRO, pers. comm.).

The collection of these two *C. albipinnum* from southeast of Albany represents a ~950 km westward range extension for this species into southern Western Australian waters (Figure 1). Anecdotal information from the crab fisher suggests they were caught regularly, i.e. a couple per month using 50–80 pots, thus there are likely reasonable numbers in this region and not just extraneous records. Swellsharks caught were released alive during normal fishing operations. This substantial

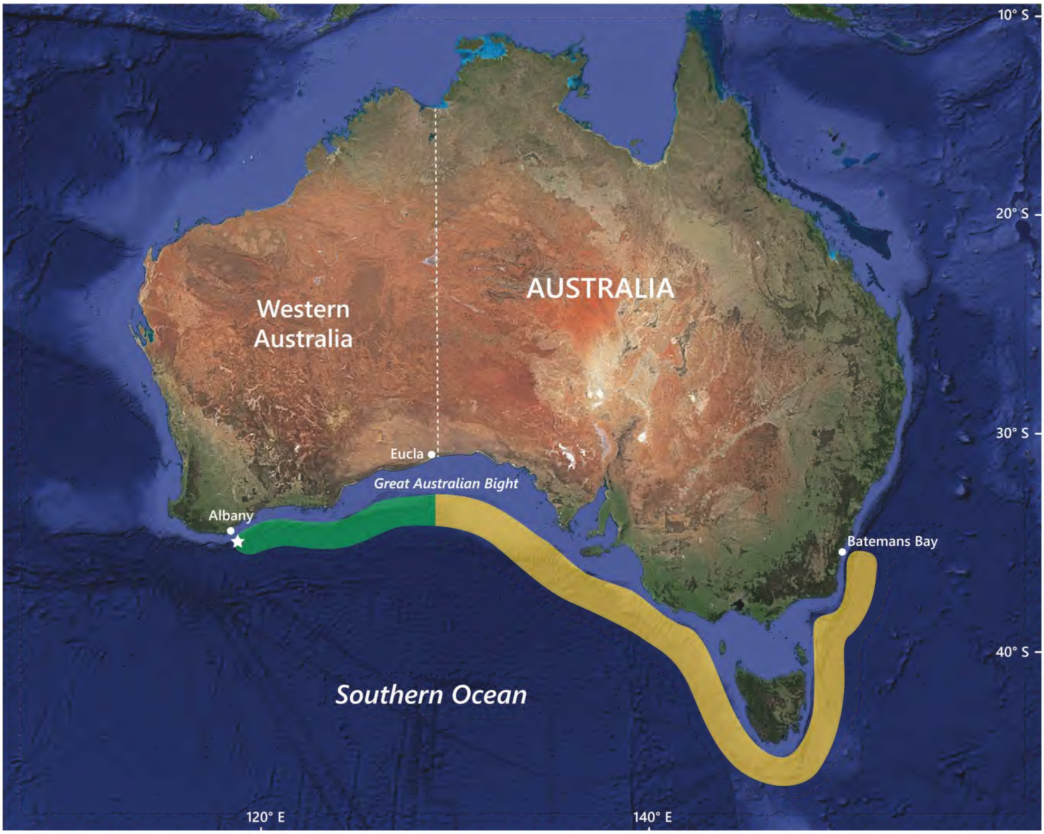

FIGURE 1 Geographic range of *Cephaloscyllium albipinnum* in southern Australia. Yellow highlighted range is the previous known range; green highlighted range is the extended distribution based on the new records (white star) (Image © Google 2023, SIO, NOAA, U.S. Navy, NGA, GEBCO).

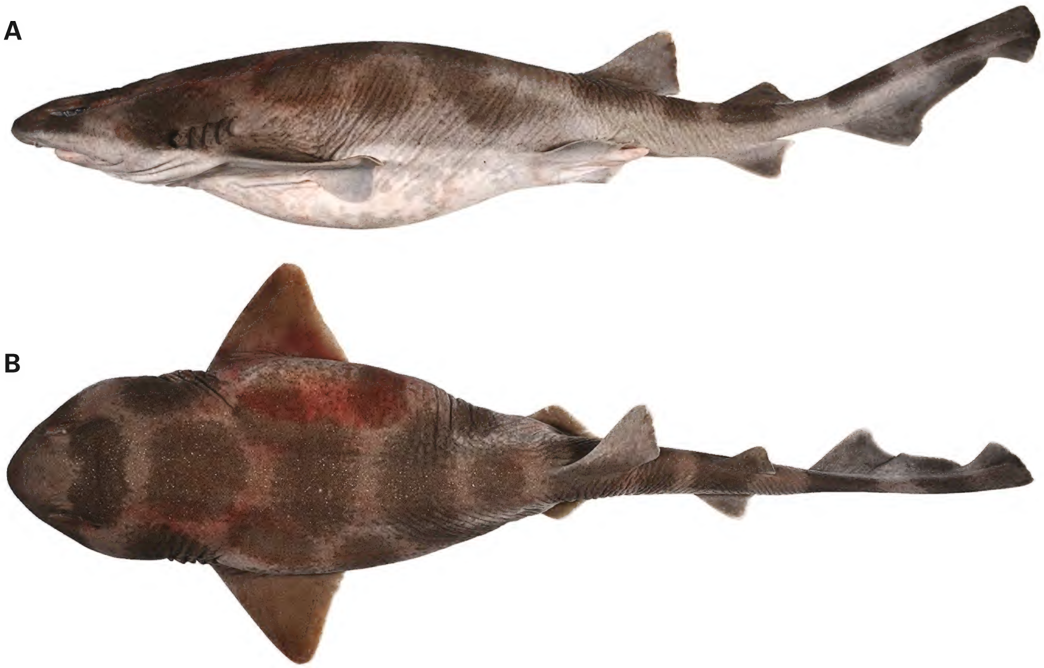

FIGURE 2 *Cephaloscyllium albipinnum* adolescent male 919 mm TL (CSIRO H 8957-01) caught south-east of Albany in 260 m depth. A) lateral view; B) dorsal view.

range extension needs to be factored into future national and international conservation assessments for this species. It is possible that this range extension expands the distribution of this species out of the more heavily exploited regions and may therefore result in downgrading of the current IUCN Red List assessment of Critically Endangered.

ACKNOWLEDGEMENTS

We are indebted to the Department of Primary Industries and Regional Development (DPIRD) for reaching out to the commercial fishers in the Albany region and facilitating the collection of the two swellshark specimens. We would like to thank Ben Hebiton, Jason How and Matias Braccini (DPIRD). Thanks also to: Leighton Matthews for providing the samples to DPIRD from his commercial crab fishing catches; Gavin Naylor and Lei Yang (Florida Museum of Natural History, USA) and Sharon Appleyard and Sahan Jayasinghe (CSIRO) for providing genetic results from the two specimens; Helen O'Neill (CSIRO) for taking and preparing images of the specimens; Alastair Graham (CSIRO) for providing registration information; and Jenelle Ritchie (WAM) for assistance with transport and registration.

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SHORT COMMUNICATION

The type locality of *Solinus pingrup* (Pseudoscorpiones: Garypinidae)

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KEYWORDS: taxonomy, Arachnida, Jarrah Forest Bioregion

As part of a recent review of the pseudoscorpion family Garypinidae, a new species of *Solinus* Chamberlin, 1930 was described from south-western Australia (Harvey 2023). The data accompanying the male holotype of *Solinus pingrup* Harvey, 2023 stated that the specimen was collected in a malaise trap at Pingrup Primary School, with two other specimens collected near North Bannister. Due to an unfortunate labelling error, the holotype was in fact collected at Allanson Primary School, some 226 km west of Pingrup, which is the true type locality.

The revised type locality is only c. 100 km from the North Bannister sites and establishes all collection localities of *Solinus pingrup* within the Jarrah Forest IBRA Bioregion (Environment Australia 2000; Thackway and Cresswell 1995), which is more compatible than the North Bannister sites in the Jarrah Forest Bioregion and the Pingrup site in the Mallee Bioregion. As implied by the bioregional names, the Jarrah Forest is dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*), tree species that are not found in the Mallee Bioregion.

The most unfortunate outcome from this error is the use of the species-group name *'pingrup'* for this species. Despite the use of the place name Pingrup, Article 18 of the International Code of Zoological Nomenclature does not allow the alteration of inappropriate names and the species-group name *Solinus pingrup* remains unchanged.

COLLECTION DATA

Australia: ***Western Australia***: ♂, Allanson Primary School, 33°20'10.4"S, 116°05'55.6"E, 8–15 March 2022, Malaise trap, Allanson Primary School students (Insect Investigators BIOUG85132-F10) (WAM T160525).

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A new bee genus and species from south-western Australia (Hymenoptera: Colletidae, Neopasiphaeinae)

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ABSTRACT – *Mimocolletes apiculus* gen. nov. and sp. nov. is described from south-western Australia. Based on morphology, this bee's closest affinities are deemed to lie with the genus *Glossurocolletes* Michener. Like the two species of that genus, *M. apiculus* appears to be oligolectic on certain pea-flowered plants (mirbelioid Fabaceae) and exhibits some morphological adaptations in common with various other colletid bees that favour pea flowers. In particular, the proboscis is slender with a strongly compressed prementum and extended glossa.

KEYWORDS: taxonomy, oligolecty, Fabaceae, morphological adaptation

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INTRODUCTION

The purpose of this paper is to make available a name for a singular species of hairy colletid bee known presently from a very limited area of south-western Australia.

The generic and family level systematics of Australia's hairy colletid bees (excluding the stenotritines – now in their own family) were well established through the monumental work of Michener (1965) in which all species were placed in the subfamily Colletinae and tribe Paracolletini. Michener retained this arrangement in his treatises of world bees (2000, 2007). Some generic-level changes were made by Maynard (1996, 1997, 2013). More recently, phylogenetic studies based on molecular data (Almeida and Danforth 2009), led to significant changes to the composition and naming of Michener's 'Paracolletini'. First, *Callomelitta* Smith was removed to a new subfamily, Callomelittinae (Almeida 2008). Second, *Paracolletes* Smith was shown to be more closely allied to the colletid subfamily Diphaglossinae than to the other taxa in the tribe. As *Paracolletes* is the type-genus, Almeida et al. (2012) resurrected the name Neopasiphaeinae Cockerell, 1930, for the bulk of the former 'Paracolletini' before Almeida et al. (2019) formally assigned *Paracolletes* to the Diphaglossinae.

I have been hesitant to create a new genus for a single species but the characters of the species in question do not permit it to be placed with certainty in any existing genus. The new taxon constitutes the third monospecific genus currently among the Australian neopasiphaeines, joining *Hesperocolletes* Michener and *Phenacolletes* Cockerell.

METHODS AND MATERIALS

All specimens are lodged in the entomology collection of the Western Australian Museum, Perth (WAM).

Abbreviations for measurements: BL body length, BMW basal width of mandible, FL flagellum length, HL head length, HW head width, LFW lower face width, ML mandible length, MOW mid-ocellus width, MSL malar space length, OOD ocellocular distance, SL scape length, SW scape width, UFW upper face width. The method of obtaining these measurements follows Houston (1975, Figs 8–9).

SYSTEMATICS

Family Colletidae

Subfamily Neopasiphaeinae

Mimocolletes Houston gen. nov.

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DEFINITION

The bees constituting this new taxon are moderately small (body lengths c. 9.5–10.0 mm), andreniform (sensu Michener 2007) and, on casual observation, look much like many other native bees having a black head and mesosoma and an orange-brown metasoma (Figures 1–2). They exhibit a particular resemblance to certain other Australian Neopasiphaeinae in having

yellow-brown appendages (Figures 1–6). On closer examination, however, they are found to possess a unique combination of characters as detailed in the following diagnosis. *Mimocolletes apiculus* is the only known species.

DIAGNOSIS

Distinguished from other genera of Neopasiphaeinae with three submarginal cells in fore wing by the following combination of characters: Pterostigma well-developed, not parallel-sided, extending into marginal cell (Figure 7); labrum evenly, gently convex, lacking transverse ridges, tubercles or carinae, median length c. 0.34 x width in male, c. 0.36 x in female (Figures 5–6); hind basitibial plates well-defined in both sexes; inner hind tibial spur of female stout, uniformly tapering to curved apex, pectinate with c. 15 teeth, longest at mid series (Figure 8). Male with T6 strongly produced apically (Figures 9–10); gonocoxites terminating apically in membranous laminae (Figure 11) that protrude from apex of metasoma (Figure 10); S7 with one pair of slender, transverse, apical lobes (Figure 12); S8 with broad, bilobed apex (Figure 13).

Morphologically, *Mimocolletes* most closely resembles *Glossurocolletes*, a genus containing only two species, both from south-western Australia. Bees of both genera share a generally stocky form, a relatively small second submarginal cell in the forewing, a mostly vertical and smooth propodeal enclosure, sexually dimorphic tarsal claws (bifid in males, simple in females), the presence of pygidial plates in males and gonocoxites bearing complex, setose laminae apically. Perhaps coincidentally, species of both genera are pea-specialists. *Mimocolletes* differs from *Glossurocolletes* in several respects enumerated in Table 1.

TYPE SPECIES

Mimocolletes apiculus sp. nov.

ETYMOLOGY

from Greek 'mimos' (= mimic; alluding to the many similarities to other genera) and *Colletes* (a genus name and common root in generic level names in Neopasiphaeinae). Masculine.

Mimocolletes apiculus Houston sp. nov.

Figures 1–18

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MATERIAL EXAMINED

Holotype

Australia: ***Western Australia***: ♂, WAM E114851, Vermin Proof Fence, 4 km S of Great Eastern Highway, Koorarawalyee, 31°18'38"S, 120°00'34"E, 20 October 2012, TFH 1405-6, on flowers of *Gastrolobium semiteres*.

Paratypes

Australia: ***Western Australia***: 2 ♀, 9 ♂, WAM E8261–E8271, 19 km ESE of Southern Cross, 31°17'38"S, 119°30'36"E, 28 October 1978, TFH 217-1, on flowers of *Gompholobium viscidulum*; 1 ♂, WAM E114852, same data as holotype.

TABLE 1 Differences between the genera *Mimocolletes* and *Glossurocolletes*.

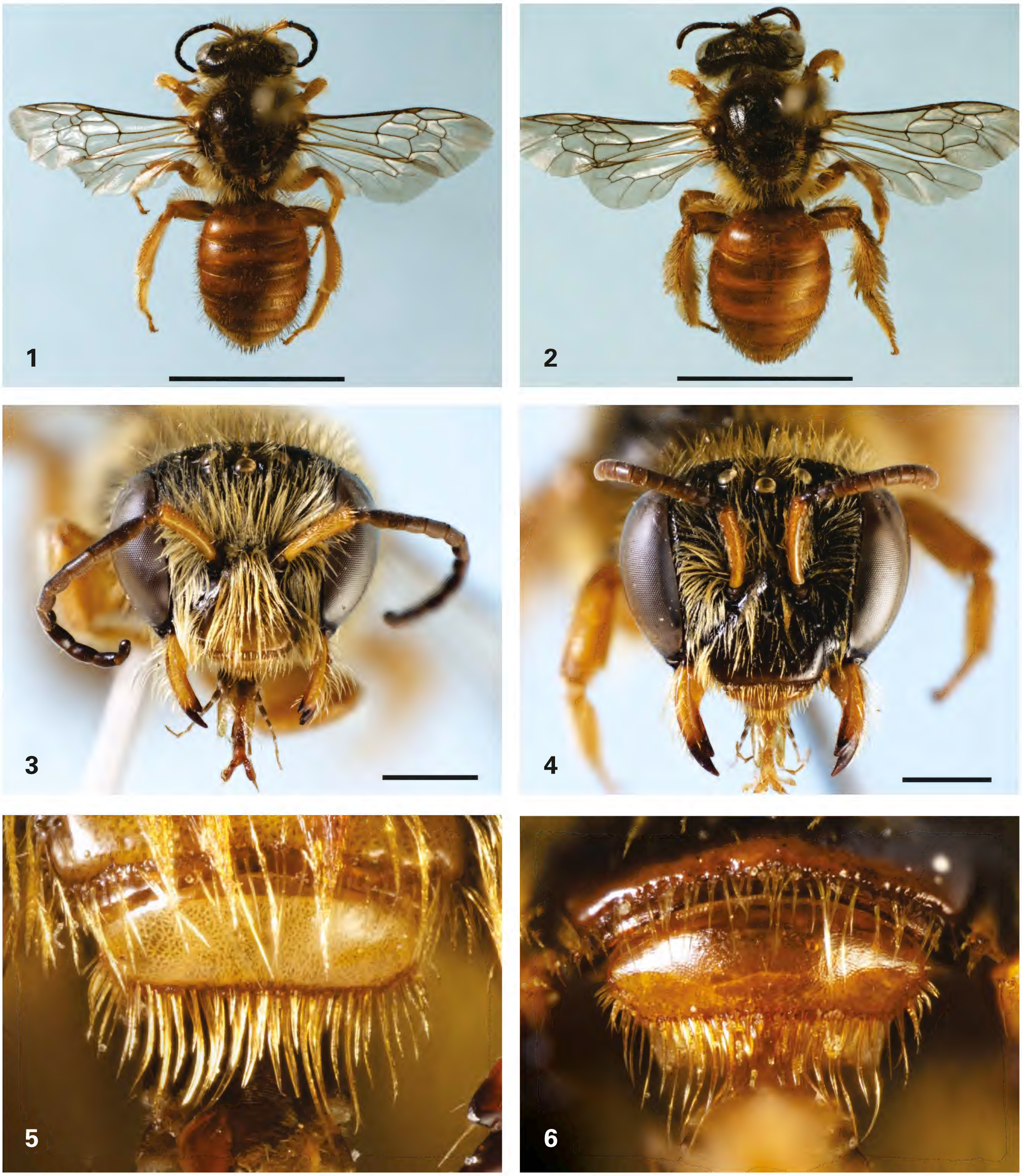
Character	*Mimocolletes*	*Glossurocolletes*
Facial foveae	Not evident	Weakly impressed
Interantennal ridge	Weak	Very strongly developed
Labrum	Moderately long and evenly, gently convex in profile	Short with strong transverse ridge basally
Metasomal hair bands	Absent	Weakly developed in female
Male scape	Slender	Thick
Male flagellum	Round in section and very slender	Dorsoventrally flattened and broad
Male S7	Apodemes well-separated; apical lobes well-developed and slender	Apodemes broadly fused; apical lobes relatively tiny
Male S8, apically	With very broad disc	With pair of stalked laminae

DESCRIPTION

Male (Holotype)

Head width 2.9 mm; body length c. 9.5 mm. Relative dimensions: HW 100; HL 76; UFW 66; LFW 54; MOW 8; OOD 17; ML 40; BMW 13; MSL 0; SL 30; SW 7; FL 106.

Head wider than long, vertex slightly higher than ocelli (Figure 3); eyes converging ventrally; gena c. 0.5 x as wide as compound eye viewed laterally; lower face rather straight in profile, clypeus gently convex transversely; supraclypeal area elevated, somewhat triangular, contiguous apically with weak median carina extending to middle of frons; malar areas obsolete; mandibles bidentate; upper margin of pronotum well below level of scutum, very thin and inconspicuous; proboscis with prementum strongly compressed, with a



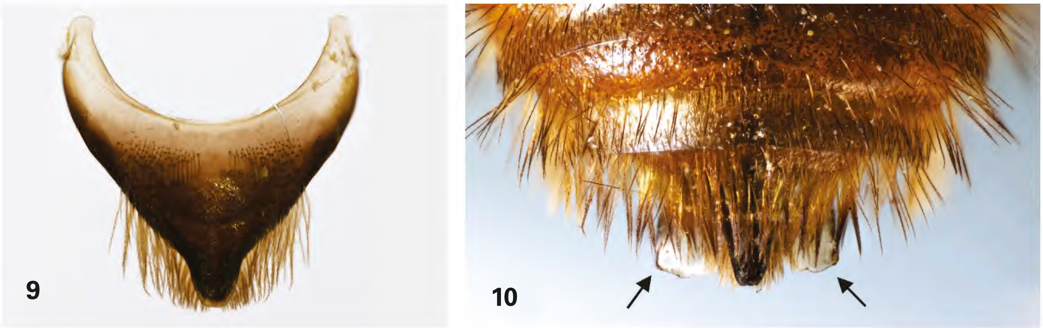
FIGURES 1–6 *Mimocolletes apiculus* sp. nov. 1) male habitus; 2) female habitus, scales = 5 mm; 3) male facial view; 4) female facial view, scales = 1 mm; 5) male labrum; 6) female labrum.

FIGURE 7 *Mimocolletes apiculus* sp. nov. wings of male (WAM E8262).

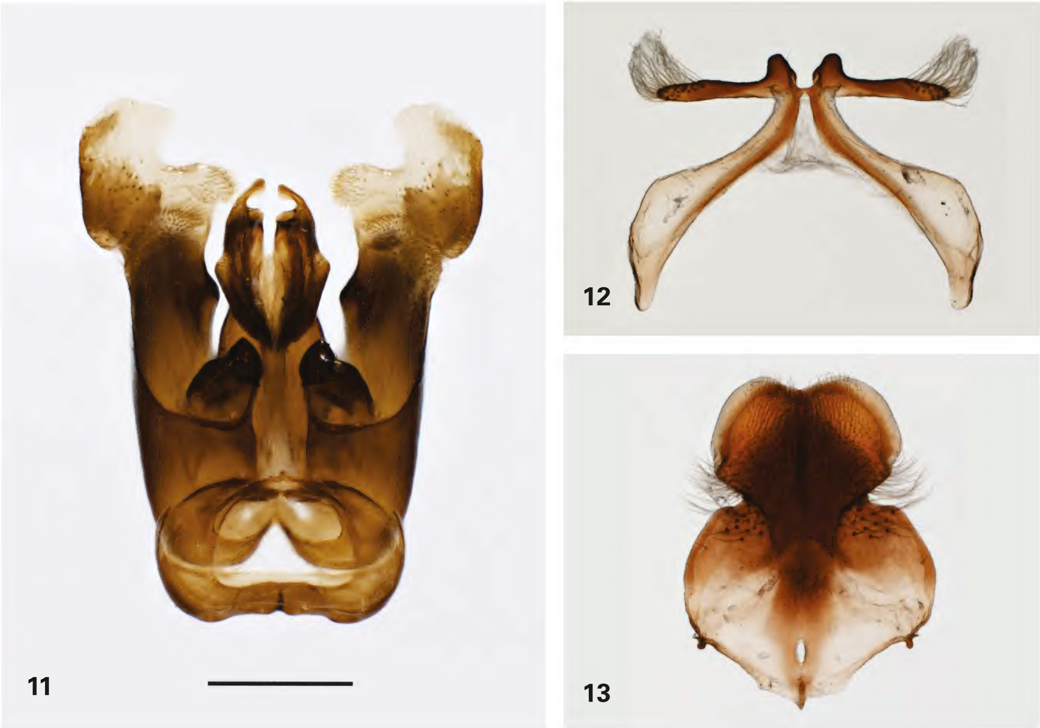
FIGURE 8 *Mimocolletes apiculus* sp. nov. inner hind tibial spur of female, scale = 0.1 mm.

median ridge posteriorly and glossa elongated (cf. female, Figure 17); antenna (Figure 14) with slender scape (length c. 4.3 x apical width) and flagellum slightly longer than head width, flagellomeres 4–10 c. 2 x longer than middle diameter, constricted basally and slightly less apically so that each has a gently convex ventral margin.

Metanotum unmodified. Propodeal enclosure with steeply sloping basal area scarcely differentiated from vertical posterior face. Legs rather short and stout; hind tibia with basitibial plate strongly defined, longer than wide and apically acute; hind basitarsus strongly compressed, nearly 1/3 as high as long; tarsal



FIGURES 9–10 Mimocolletes apiculus sp. nov., male: 9) apical (7th) metasomal tergum showing protuberant pygidial plate; 10) apex of metasoma in dorsal view showing protuberant, black, pygidial plate medially (on either side of the latter, indicated by arrows, are the apical laminae of the gonocoxites).



FIGURES 11–13 *Mimocolletes apiculus* sp. nov., male: 11) genital capsule, ventral view; 12–13) seventh and eight metasomal sterna, respectively, in dorsal view. Scale = 0.5 mm.

claws (Figure 15) bifid, prongs subequal, closely approximated; arolia present. Metasomal T1 with abrupt anterior face rounding onto dorsal surface; T2 with no lateral foveae; T2–T5 with graduli strongly impressed with anterior margin of each gradulus developed into a thin, transparent, posteriorly directed lamina; hind margins of T1–T5 wide and transparent.

Pubescence: compound eyes with a few scattered, peg-like setae between the ommatidia; head and mesosoma generally clothed in moderately dense, long, erect, plumose, straw-coloured setae; similar pubescence on bases of fore legs; mid and hind legs with shorter, sparser setae; metasomal terga with sparse, erect, simple, black setae; T6 and T7 with long, plumose, golden setae laterally; sterna with very short setae, lacking apical fringes.

Colouration: integument of head and mesothorax largely black; the following are yellow-brown: lower 1/3

FIGURE 14 *Mimocolletes apiculus* sp. nov., male, left antenna.

FIGURES 15–16 *Mimocolletes apiculus* sp. nov. apical views of distitarsi showing dimorphism of claws: 15) male; 16) female.

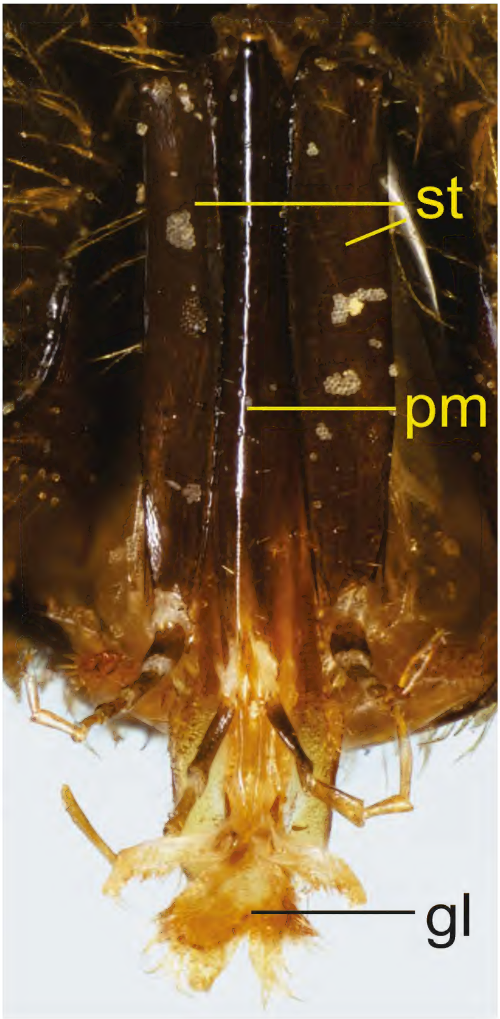


FIGURE 17 *Mimocolletes apiculus* sp. nov. posterior view of proboscis of female (gl, glossa; pm, prementum with median edge reflecting light; st, stipites).

of clypeus, grading to black above; labrum, mandibles (except for blackish apices) and scapes; the following are orange-brown: legs below trochanters, metasoma (except for black apex of T7). Antennal pedicel and flagellum dark brown; tegulae and wings veins light to dark brown.

Sculpture: clypeus laterally, ventrally and medially glossy, lacking pitting, but with a pair of pitted paramedian patches; integument of remainder of head, mesosoma and metasoma generally shining with small open pitting and minute pitting in the interspaces; propodeal enclosure smooth, glossy, lacking carinae.

Terminalia: See generic diagnosis and Figures 11–13.

FIGURE 18 *Mimocolletes apiculus* sp. nov. female, apex of femur and base of tibia of hind leg showing apically acute basitibial plate.

Female (WAM E8271)

Head width 3.3 mm, head length 2.5 mm; body length c. 9.9 mm. Relative dimensions: HW 100, HL 75, UFW 67, LFW 56, MOW 7, OOD 18, SL 30, SW 6.

For the most part similar in form to male, sharing with it a strongly compressed prementum and a slender, elongated glossa (Figure 17), but differing as follows: flagellum little more than half as long as head width, middle flagellomeres about as long as wide; upper margin of pronotum developed into a projecting angle each side; tarsal claws stout but simple (Figure 16); basitibial plate c. 0.3 x as long as hind tibia, acute at apex (Figure 18); pygidial plate small, flat, apically rounded.

Pubescence: as in male except as follows: setae on dorsum of mesosoma shorter, less dense in centre of scutum; scopa developed on hind coxae, trochanters, femora (except ventrally), tibiae and basitarsi, consisting of long, dense, highly branched golden-brown setae; metasomal sterna largely covered with long, erect, weakly plumose setae; prepygidial and pygidial fimbriae consisting of long, dense, plumose, gold-brown setae.

Colouration: as for male but clypeus largely black, only ventral margin somewhat brownish (Figures 4, 6).

Sculpture: Much as in male. Clypeus with close, fine pitting either side of midline, otherwise sparsely pitted and shining.

DISTRIBUTION

This species is recorded from only two localities 47 km apart and situated between Southern Cross and Coolgardie, Western Australia (Figure 19). One of the recorded forage plants, *Gompholobium viscidulum* Meisn., has a wide distribution in south-western Australia, extending from the Southern Cross region

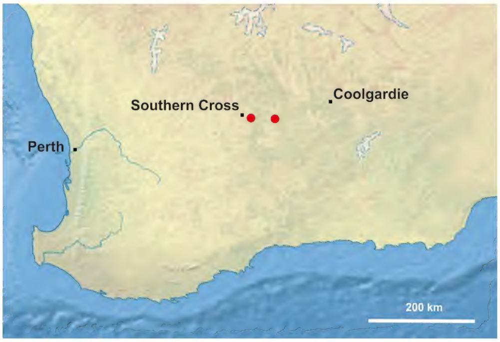


FIGURE 19 Collection localities of *Mimocolletes apiculus* (solid circles) in south-western Australia.

south to near Albany and east almost to Cape Arid (AVH 2024a). The other, *Gastrolobium semiteres* Chandler & Crisp, is known from far fewer localities, mainly in the Southern Cross — Boorabbin region, but is recorded also from c. 110 km south-east of the bee's known range (AVH 2024b). Potentially, the bee's actual geographic range could be much more extensive than currently known.

ETYMOLOGY

From Latin 'apiculus' (= extended to a point), alluding to attenuated apex of metasoma of male.

DISCUSSION

As reflected by its name, *Mimocolletes* shares numerous features with other Neopasiphaeinae. Like *Hesperocolletes* and *Trichocolletes*, it possesses a relatively large, evenly convex labrum which distinguishes it from *Leioproctus*. The narrow and strongly compressed prementum and stout inner hind tibial spur are shared with various other pea-flower specialists, such as *Glossurocolletes* and some *Trichocolletes* species, and may be adaptive. The slender, compressed prementum might facilitate insertion of the glossa between bundles of stamens to reach the nectary. Because only some species of *Trichocolletes* favouring pea-flowers exhibit this feature, it seems best not to treat it as a generic characteristic in *Mimocolletes*. Sexually dimorphic tarsal claws occur also in at least some species of *Leioproctus* (*Cladocerapis*) and *Trichocolletes*.

The orange-brown antennal scapes of both sexes and the yellow-brown clypeus of the male (less so the female) are seen in just some species of various other neopasiphaeine genera such as *Anthoglossa*, *Chrysocolletes, Hesperocolletes, Leioproctus* and *Trichocolletes*. The male terminalia, however, are quite distinctive.

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Patterns of gastropod predation on middle Eocene echinoids from the western Eucla Basin, Western Australia

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ABSTRACT – Modern echinoids are known to suffer predation from a range of organisms, from fishes to gastropods and sea otters to birds. One of the most common evidence for such predatory behaviour in the fossil record comes from the ichnospecies *Oichnus simplex* Bromley, 1981, a small, straight-sided, circular hole which in the test of echinoids is interpreted as having been made by cassid gastropods. Such trace fossils provide good evidence for the temporal and geographical distribution of these gastropods in the past. Here we report such gastropod predation on a diverse middle Eocene echinoid fauna from bryozoal limestones in southwestern Australia. Of the 14 species of echinoids recorded, half show evidence of such predation. All are irregular echinoids that burrowed in the sediment to varying degrees. The percentage of echinoid specimens that suffered gastropod predation is 8.3%, varying between 6% and 16% of those echinoids for which there are statistically significant samples. The presence of what is interpreted as cassid predation on these middle Eocene echinoids is the earliest record in Australia and one of the earliest known in the evolutionary history of the group, marking the beginning of the expansion of this form of gastropod predation on echinoids.

KEYWORDS: Echinoidea, Gastropoda, Cassidae, Eocene, predation, palaeoecology, Western Australia

INTRODUCTION

Evidence from a number of echinoid faunas of Oligocene and Miocene age in southern Australia indicates that they suffered, often heavily, from predation by gastropods (McNamara 1994). Between one-third and almost two-thirds of the early Miocene echinoids experienced lethal predation, most likely from cassid gastropods. However, McNamara (1994, p. 786) indicated that none of the Eocene echinoid faunas from southern Australia appeared to show evidence of such predation by these gastropods. This seemed to support the view at the time that cassid gastropods were not present in Australia until the late Oligocene (Darragh 1985). However, in light of the revelation that cassids were indeed present in Australia in the middle–late Eocene of the Southern Carnarvon Basin (Darragh and Kendrick 2008) and in the late Eocene of Victoria (Darragh 2023), it is timely to reassess the evidence from echinoids of cassid predation during the Eocene.

In this paper we present evidence of predation upon echinoids from middle Eocene limestones of the Esperence Shelf, Eucla Basin, Western Australia. These echinoids show the presence of the ichnospecies *Oichnus simplex* Bromley, 1981, a small, circular, parallel-sided hole in the test, interpreted as a result of predatory activity by cassid gastropods. This record represents not only the earliest evidence of gastropod predation on echinoids in Australia, but also accords with the revised first occurrence of cassid gastropods in the region.

Predation within echinoid communities, although probably common during the Cenozoic, has not been particularly well-documented. Amongst case studies, McNamara (1994) has reviewed the occurrence and trends of gastropod predation on Oligocene and Miocene echinoids in southern Australia. Meadows et al. (2015) have described such predation in Oligocene echinoids from New Zealand. Ceranka and Złotnik (2003) and Kowalewski and Nebelsick (2003) have documented predation in Miocene echinoids from Poland, and Mancosu et al. (2022) in Miocene echinoids from Sardinia. Grun et al. (2017) have described

drilling predation in living *Echinocyamus* from the Mediterranean Sea. The taphonomic legacy of predation on echinoids has been examined by Nebelsick (1999), whereas predation-facilitated preservation of echinoids has been studied by Tyler et al. (2018).

The only other detailed case study of gastropod predation on Eocene echinoids is by Gibson and Watson (1989) on echinoids from the upper Eocene Ocala Formation in the United States. Attempts to carry out a broad review of gastropod–echinoid predator–prey relationships on the basis of the literature and museum collections has been recently undertaken by Farrar et al. (2020) and Petsios et al. (2021). The documentation of what we interpret as largely cassid gastropod predation on Eucla Basin middle Eocene echinoids would appear to represent the earliest recorded example of such predation worldwide. As such, it provides additional data to test the views of Farrar et al. (2020) and Petsios et al. (2021) on the significance of gastropod predation to patterns of evolution in irregular echinoids as a whole.

What these studies all show is that patterns of predation, as shown by trace fossil evidence, can play an important role in both palaeoecological and evolutionary studies, being one of the few biological interactions between taxa that can be readily observed and interpreted in the fossil record. Modern-day gastropod–echinoid predator–prey relationships have been studied by Hughes and Hughes (1971, 1981) and Hughes (1986), making it is possible to infer that cassid gastropods were responsible for much of the demonstrable predation on echinoids seen in the fossil record, on account of their characteristic method of predation. Hughes (1986) has described the hunting method used by the modern cassid species *Galeodea echinophora* (Linnaeus, 1758) to prey upon the infaunal echinoid *Echinocardium cordatum* (Pennant, 1777). This technique is likely to have been similar to the method employed by cassids from the Eocene to the present day, based on corroboratory evidence we present here on a failed predation attempt. In living forms, the gastropod locates the infaunal echinoid by olfactory means, then begins its attack by inserting its proboscis into the sediment. Although some echinoids remain buried throughout the attack, most try to flee by rising to the surface, whereupon the cassid covers the echinoid with its foot, then makes an incision, both by secretion of sulphuric acid and by cutting a circular disc with its radula. The incised disc is pushed into the echinoid's body cavity and the proboscis inserted and elements of the viscera (usually the gonads) sucked out. Because of this distinctive predatory technique, the gastropod's activity can be relatively easily identified from the usually neat, round hole with characteristic parallel sides they leave behind. Although most of the boreholes identified in this study show this morphology, a few are bevelled or stepped, suggesting other types of predatory gastropods may also have been attacking the echinoids.

Although McNamara (1994, p.786) noted that the 'examination of…echinoids from the Late [sic.] Eocene Nanarup Limestone…has shown no evidence of gastropod predation' a re-examination of this biota has revealed that some echinoids do indeed possess the trace fossil *Oichnus simplex* in their tests, indicative of having been preyed upon by gastropods. In this paper we document the evidence for gastropod predation within the echinoids from the middle Eocene limestones from the western Eucla Basin, investigating variability in borehole morphology and placement, discuss species and test area selection phenomena, and the relevance of water depth to predation levels.

GEOLOGICAL SETTING

Within the Esperance Shelf (western Eucla Basin), middle Eocene echinoids are recorded in two lithostratigraphic units exposed east of Albany: the Nanarup Limestone and an unnamed limestone at Manypeaks (see McNamara and Martin 2022, Figure 1). The Nanarup Limestone is a yellow to white, friable medium-grained bryozoal grainstone, with minor siltier packstone. It lies conformably beneath the Werillup Formation (Quilty 1981; Clarke et al. 2003). The unit is best seen preserved in a limestone quarry at Nanarup 17 km east of Albany, and is about three metres in thickness (McNamara and Martin 2022). Another, more silty, limestone of comparable age occurs at Manypeaks, 20 km northeast of Nanarup. Known informally as the 'Manypeaks limestone', echinoids from this unit also form part of this study. The echinoid faunas from the two limestones have been described elsewhere (McNamara and Martin 2022).

The limestones were deposited as part of the Tortachilla Transgression. This has been dated as middle Eocene (Bartonian) in age based on foraminiferal evidence, and corresponds to planktonic foraminiferal zones P14–15 (Li et al. 2003). The unit is highly fossiliferous; in addition to the echinoids, the fauna contains bryozoans, brachiopods (Craig 1997, 2001), bivalves, gastropods, asteroids, crinoids (Whittle et al. 2018), foraminifers (Quilty 1969, 1981), nautiloids, sponges, crabs and rare shark teeth. A study of brachiopods from the Nanarup Limestone (Tuura et al. 2008) revealed that they too suffered some predation by gastropods, possibly muricids, with up to 16% of individuals showing evidence of having been drilled.

MATERIAL AND METHODS

The echinoid faunas of the Nanarup Limestone and Manypeaks limestone are relatively diverse, with a total of 14 recorded species. The fauna of the Nanarup Limestone comprises: *Temnocidaris* (*Stereocidaris*) *cudmorei* Philip, 1964, *Ortholophus* aff. *bittneri* Phillip, 1969, *Pleurosalenia tertiaria* (Tate, 1877),

Eurhodia westaustraliae McNamara & Martin, 2022, *Australanthus longianus* (Gregory, 1890), *Echinolampas posterocrassa* (Gregory, 1890), *Fossulaster susae* McNamara & Martin, 2022, *Cyclaster jamiei* McNamara & Martin, 2022, ?*Isaster* sp., micrasterid indet., *Hemiaster (Bolbaster) subidus* McNamara, 1987, *Schizaster (Paraster)* cf. *tatei* McNamara & Philip, 1980, *Protenaster preaustralis* McNamara, 1985 and *Gillechinus kaitae* McNamara & Martin, 2022. Of these, all bar *B. subidus, P. preaustralis, S. (Paraster)* cf. *tatei*, ?*Isaster* sp. and micrasterid indet. also occur in the Manypeaks limestone.

A total of 551 whole, partial and fragmentary non-cidaroid tests, innumerable cidaroid spines and loose plates, and over 70 *T.* (*Stereocidaris*) *cudmorei* fragments from the Nanarup Limestone housed in the Western Australian Museum (WAM) collection were used in this study. However, the large number of specimens is deceptive, as the fauna is dominated by two forms — the echinolampadoid *Echinolampas posterocrassa* and the cidaroid *T.* (*Stereocidaris*) *cudmorei*. The Manypeaks limestone yielded 38 non-cidaroid tests and 2 cidaroid fragments.

We follow the terminology of Gibson and Watson (1989) to describe the trace fossils, with boreholes being classified according to their orientation relative to the test (normal or inclined), surface expression (rounded or irregular), penetration (penetrative or non-penetrative), and the nature of the borehole wall (parallel, bevelled or stepped). In addition to this, the placement of the borehole was noted, including the 'side' — ie. aborally, adorally or ambitally — and the area of the test, identified using the standard nomenclature for test plating (Lovén 1874), with the five interambulacral series numbered wth Arabic numerals 1–5 and the ambulacral series with Roman numerals I–V.

If it is assumed that each partial or fragmentary specimen represents the remains, albeit incomplete, of a whole individual, the calculated percentages of the population that have undergone predation will be an underestimate, as a partial test lacking an incision may actually have been bored, with the bore occurring on the missing part. As a result, to provide more accurate assessment of predation levels in the fauna, partial tests are considered to represent half an individual, with fragmentary tests representing a quarter. Therefore, one whole test, two partial tests, or four fragmentary tests may each be considered to represent one individual. Using this, the number of specimen equivalents for each species can be established. Thus two percentages of predation for each species are presented, one based on the percentage of total specimens bored, irrespective of whether complete, partial or fragmentary, and a second percentage (presented in italics in parentheses) based on specimen equivalents.

RESULTS

Of the 668 echinoid specimens (396.5 specimen equivalents) from the middle Eocene Nanarup and Manypeaks limestones used in this study, 55 were observed to have circular, parallel-sided incisions. All, bar one, appear to pass through the entire test and were therefore assumed to have resulted in lethal predation by cassid gastropods. This equates to 8.2% (*13.9%*) of the echinoids having suffered active gastropod predation. Of the 14 species of echinoids present in the Nanarup Limestone and the Manypeaks limestone (McNamara and Martin 2022), seven show evidence of gastropod predation. These are the cassiduloids *Eurhodia westaustraliae* and *Australanthus longianus,* the echinolampadoid *Echinolampas posterocrassa* and the spatangoids *Cyclaster jamiei*, ?*Isaster* sp., *Hemiaster (Bolbaster) subidus* and *Gillechinus kaitae*.

Order Cassiduloida
L. Agassiz & Desor, 1847

Eurhodia westaustraliae
McNamara & Martin, 2022

REMARKS

Four partially preserved specimens of this species are known from the Nanarup Limestone, with a further specimen from the Manypeaks limestone. Of these, one of the Nanarup tests (WAM 07.439) possesses a single, rounded borehole with parallel sides. It is inclined at an angle of 20° from normal towards the anterior and is penetrative. The borehole is relatively large, being about 3.5 mm in diameter (7% TL), and occurs on the anterolateral ambitus of the test (Figure 1A). As the hole is single and penetrative, the echinoid is likely to have suffered a lethal, predatory gastropod attack. Later species of *Eurhodia* appear to have been more susceptible to cassid predation — *E. australiae* (Duncan, 1877) from the upper Oligocene Jan Juc Formation has been shown to have suffered higher levels of predation, with 37% from a sample number of 40 specimens having been bored (McNamara 1994).

Australanthus longianus
(Gregory, 1890)

REMARKS

Of the 25 specimens of this species known from the Nanarup and Manypeaks limestones, four, all from the Nanarup Limestone, show evidence of gastropod predation. Two specimens have a single borehole, the other two each have a pair. The holes are relatively small, varying between 1.29 mm and 2 mm in diameter. In all specimens boreholes are located on the adoral surface of the test, mainly close to the ambitus. In shape they are round or slightly elongate, and half inclined. Whereas one is bevelled, the others are parallel-sided and likely made by cassid gastropods.

Order Echinolampadoida Kroh & Smith, 2010

Echinolampas posterocrassa Gregory, 1890

REMARKS

This is the most common species in the Nanarup Limestone, with 385 whole and partial tests used in this study (212 specimen equivalents). Many of the Nanarup specimens have been bored, the boreholes varying somewhat in morphology. Forty-four specimens have one or more boreholes. Of these, 19 have multiple boreholes, ranging from 2 to 11 per test and showing a large range of diameters. The smallest is 0.55 mm and the largest is 3.70 mm, with an average of 1.61 mm. Of these, 48% of the boreholes occur on the aboral surface of the test and 52% on the adoral surface. In terms of their distribution, on the adoral surface most boring occurred around the ambitus (Figure 1C), and mainly toward the anterior, although two distinct groups do occur on interambulacra I and IV. Aborally the pattern is less coherent, although the boreholes also tend to be concentrated towards the ambitus (Figure 1B), as well as along the midline of the test. The apical and ambulacal areas are generally not bored.

Four borehole geometries are present in *E. posterocrassa*. The first, and most common, are the circular, straight-sided boreholes (67.9% of bored specimens), and thus attributed to the predatory activity of cassid gatropods. Some elongate boreholes also occur, which are interpreted as representing circular boreholes incised on an inclination to the surface of the test (17.3%). These too are attributed to the activity of cassids. Irregular boreholes are also present, which have ragged edges (9.9%); these are most common on the adoral surface of the test. Finally, two of the specimens possess 'tandem' holes, which appear as two rounded boreholes placed next to one another and connected (4.9%). Most of the boreholes are vertical or normal to the test, but 21% are inclined; these are more common on the aboral surface (65.7% of inclined boreholes). Although most boreholes are vertical, two are stepped (with two distinct bore sizes within the same bore), and nine are bevelled. These represent 2.5% and 11.1% of the bored specimens respectively.

Of the 44 specimens wth boreholes, 16 have multiple incisions, ranging from seven specimens with two traces, to one specimen with 11 boreholes. When compared with specimens with single boreholes, in those with multiple boreholes, the diameters are appreciably less, averaging 1.61 mm compared with 1.89 mm in specimens with just a single hole. Significantly, in specimens with multiple borings, one borehole is consistently larger than the others. If those tests with multiple boreholes are considered to have been bored mainly post-mortem, it is possible that one of the boreholes represents a lethal boring, and the others are evidence of post-mortem scavenging activity, either by the same individual, or by other gastropods. Usually specimens with multiple borings also possess evidence of extensive epibiont activity, in the form of colonies of bryozoans and serpulids (see McNamara and Martin 2022, figure 12). This indicates exposure of the test for a relatively long post-mortem period, prior to re-burial and eventual fossilisation, which would have provided opportunistic situations for scavenging gastropods. Those specimens possessing a single borehole are rarely covered by epibionts, suggesting predation while buried in the sediment. Of the total studied collection of *Echinolampas posterocrassa* at Nanarup, 11.4% (*20.7%*) have boreholes. Specimens with single boreholes comprise 6.9% of specimens. In terms of distribution, adoral borings are the most common, comprising 62.5% of single-bored tests. In terms of their distribution, the ambital region of the test is most commonly bored. 16.7% of boreholes are irregular in shape, none of which are tandem and a similar percentage are inclined; these inclined examples are all circular or elongate in shape. Although most of the boreholes are parallel sided, three (12.5%) are bevelled, suggesting other groups of gastropods may have been involved in similar predatory behaviour.

Five specimens of *E. posterocrassa* are known from the Manypeaks limestone. Only one is bored. This specimen has a single borehole, which occurs aborally in between ambulacra IV and V. The borehole is vertical, round and parallel-sided. Compared with the size of the test (TL = 31.7 mm), the bore is rather large, occupying about 10%TL (borehole diameter 3.52 mm). The hole is slightly distorted by test fracturing, but appears penetrative.

Order Spatangoida L. Agassiz, 1840

Cyclaster jamiei McNamara & Martin, 2022

REMARKS

Of the four known specimens of this species, one (WAM 03.12) possesses a circular borehole, located on the aboral surface close to the ambitus in interambulacrum 4 (Figure 1D). It is small, with an outer diameter of 1.45 mm. The direction of boring is perpendicular to the surface of the test. However, not only does the boring fail to penetrate the test, but the area surrounding the borehole shows evidence supporting the notion of a failed attempt, and demonstrating the method of boring used by the predator.

The borehole only penetrates partially through the test and narrows progressively away from the outer test surface. It is surrounded by an areola of smooth test (Figure 1E), the spines and tubercles having been removed during the process of predation. The diameter

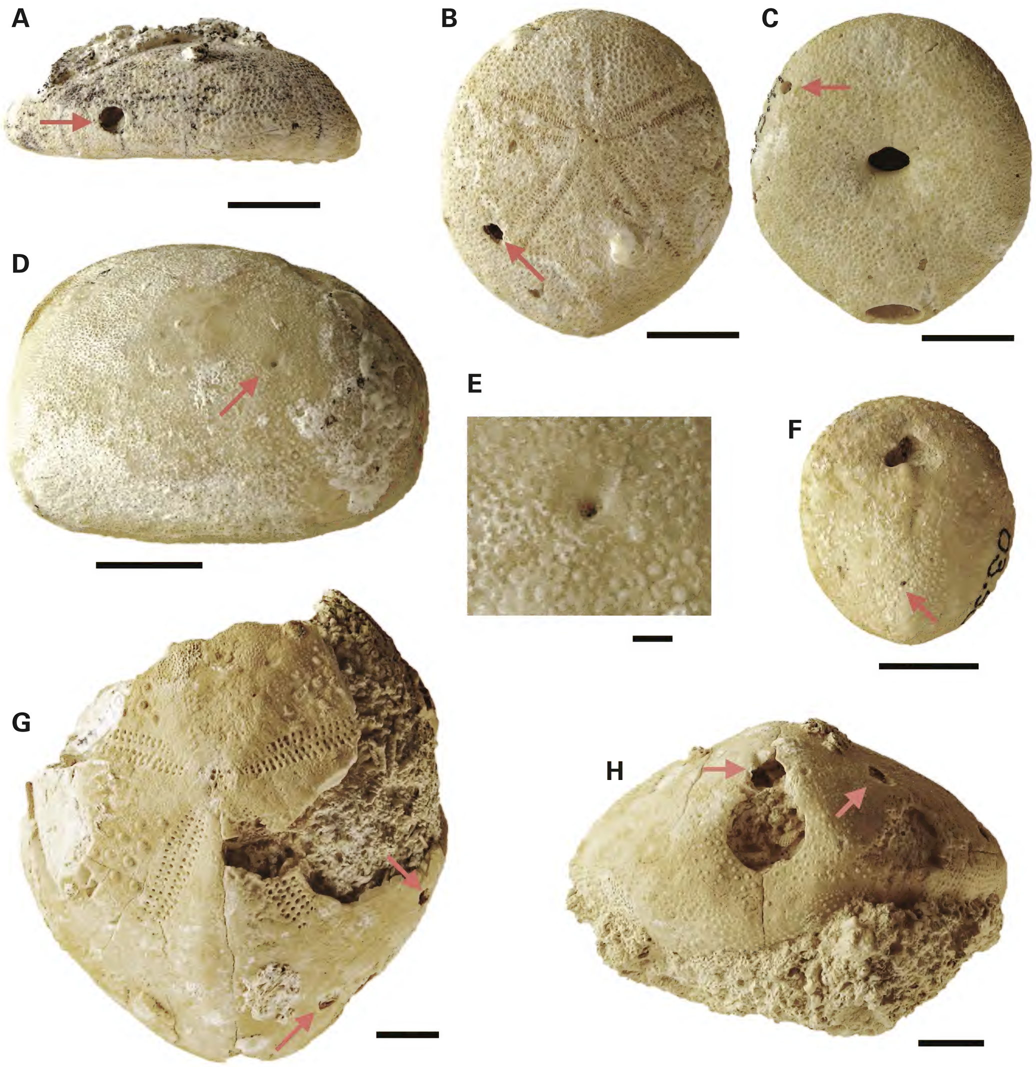

FIGURE 1 A) *Eurhodia westaustraliae*, lateral view of WAM 07.439, scale = 10 mm; B–C) *Echinolampas posterocrassa*, aboral and adoral views, respectively, of WAM 03.41, scale = 10 mm; D–E) *Cyclaster jamiei*, lateral views of WAM 03.12, scale = 10 mm and 1 mm respectively; F) *Hemiaster (Bolbaster) subidus*, aboral view of WAM 03.50, scale = 10 mm; G–H) *Gillechinus kaitae*, aboral and posterior views, respectively, of WAM 07.444, scale = 10 mm. All specimens from the Nanarup Limestone. Arrows point to locations of cassid predation incisions.

of the areola is about 4 mm. It is considered that the smooth area around the borehole was formed by dissolution following acid secretion by the proboscis of the gastropod, removing the tubercles in the process. Such evidence of predatory behaviour with an acid-etched areole has been described in the living species *Echinocyamus crispus* Mazzetti, 1893 (Nebelsick and Kowaleski 1999). Hughes and Hughes (1981) have demonstrated how living cassids make incisions in echinoid tests by a combination of mechanical drilling by the proboscis and secretions of sulphuric acid that weaken the test surface, making the drilling easier. What the specimen of *C. jamiei* appears to demonstate is that the gastropod would have removed the spines to expose the test, then simultaneously begun to mechanically drill and acid-etch the test surface, removing the outer surface and the tubercles. During successful predation, a disc would be cut and forced into the test, making an opening through which the proboscis could be inserted. In this case, the gastropod must have been disturbed in the early phase of its predatory activity.

?*Isaster* sp.

REMARKS

Two incomplete specimens of this species are known from the Nanarup Limestone. In one (WAM 03.52) a small (1.2 mm in diameter) circular borehole is present in interambulacrum 2 on the adoral surface of the test. The hole is circular and parallel-sided. It is slightly inclined and penetrative, indicating successful predation.

Micrasterid indet.

REMARKS

A single specimen of this form (WAM 07.431) has a small, elongate incision, the longer axis being 1.1 mm, located close to the apical disc in interambulacrum 5 (see McNamara and Martin 2022, Figure 8). The specimen is partially encrusted by bryozoans, suggesting that the incision may have been made post-mortem, possibly by a clionid sponge.

Hemiaster (Bolbaster) subidus McNamara, 1987

REMARKS

Two specimens of this species are known from the Nanarup Limestone. One (WAM 03.50) has a single, small, circular hole 1.67 mm in diameter on the adoral surface of the test, located on the midpoint of the plastron, close to the sagittal line (Figure 1F). The borehole is penetrative, normal to the test, and is parallel-sided, typical of cassid predation.

Gillechinus kaitae McNamara & Martin, 2022

REMARKS

Twenty-eight partial and fragmentary specimens of this species are known from the Nanarup Limestone, and 19 whole, partial and fragmentary specimens from the Manypeaks limestone. None of the Manypeaks limestone *Gillechinus* specimens shows any evidence of predation. Three Nanarup Limestone specimens show evidence of gastropod predation. Two are partially preserved tests, each with a single, sizeable borehole. Both of these boreholes are normal to the test, 2.6 and 2.8 mm in diameter, and parallel-sided. In one specimen, the hole is round and occurs on the adoral side of the test in interambulacrum 2; in the other, the bore is rounded but irregularly edged and occurs aborally in interambulaum 1. Although the specimen with the adoral borehole has part of this hole broken, its break appears to postdate the incision, and therefore may be post-predation. Although encrustation by epibionts indicates a period of post-mortem exposure of the specimen, these boreholes are most likely to represent successful gastropod predation. The third specimen (WAM 07.444) has three boreholes. The largest is a circular incision 5.2 mm in diameter, located immediately above the periproct (Figure 1H). Another, 3.3 mm in diameter, is located on the aboral surface, at the margin between interambularum 5b and ambulcarum Ia, close to the ambitus (Figure 1G,H). The third, 2.5 mm in diameter, is located almost on the ambitus in interambulcrum 1 (Figure 1G).

DISCUSSION

Given that 50% of the echinoid species recorded from the middle Eocene Nanarup and Manypeaks limestones show typical gastropod predation boreholes, this demonstrates that predation pressure on echinoids from gastropods was widespread during the middle Eocene off the southwestern corner of the Australian continent. The most common borehole morphology, consisting of a circular hole with parallel sides, is typical of that found in the tests of modern-day echinoids that have suffered cassid gastropod predation (Hughes 1986; Hughes and Hughes 1971, 1981). The far more uncommon bevelled boreholes could possibly have been made by the predatory activity of naticid gastropods.

McNamara (1994) had previously argued that the earliest evidence for cassid gastropod predation in the Cenozoic of Australia was in the upper Oligocene Jan Juc Formation in Victoria. However, this present study shows much earlier evidence of such predation, with the implication being that cassids were present in Australia 15 million years earlier than previously interpreted, within the Paleogene. This is supported by the discovery of the cassid ?*Galeodea* sp. in a middle–upper Eocene deposit in the Southern Carnarvon Basin near Kalbarri (Darragh and Kendrick 2008). Although cassid fossils have yet to be found in the Nanarup and Manypeaks limestones, gastropod fossils in those units are not very common, likely due to taphonomic reasons. Therefore, the discovery of ?*Galeodea* sp. confirms the presence of cassids off the western Australian continent at the time of these limestones' deposition in the Eucla Basin further south. Interestingly, the rich, largely undescribed, echinoid fauna from the upper Paleocene Cardabia Formation of the Southern Carnarvon Basin in the Giralia Range area shows no evidence of having suffered gastropod predation (McNamara in prep), indicating that cassids were not present in the region at that time.

The predation levels vary appreciably between the seven incised species in the Nanarup and Manypeaks limestones. This is in part due to the variability in number of specimens of each species, but, at least for the most common species, this variability was also likely a reflection of fundamental biological and ecological differences between species. Three of the seven predated species — *Australanthus longianus* (n=25), *Echinolampas postercrassa* (n=385) and *Gillechinus*

kaitae (n=47) — have meaningfully large sample numbers that allow a relatively accurate assessment to be made of variations in the extent to which cassids preyed upon susceptible echinoids. The most common of these three species, *E. posterocrassa*, is likely to have been a burrowing echinoid, based on the reported behaviour of modern species of *Echinolampas* (Thum and Allen 1976; Mooi 1990). Despite this, 11% (*21%*) suffered predation by cassids. For an Eocene species of *Echinolampas* to have been killed by cassid activity suggests that, even early in the evolutionary history of this gastropod family, they had the ability to undertake infaunal predatory behaviour such as is commonly seen in modern cassids (Hughes and Hughes 1971, 1981). Of the three most common echinoid species, *Australanthus longianus* suffered the highest levels of cassid predation, with 16% (*38%*) of specimens having been bored; nothing is known about the burrowing behaviour of this genus. The third species, *Gillechinus kaitae*, has the lowest levels, with 6% (*15%*) cassid predation. One reason for this might be the presence of large primary spines on the aboral surface of this maretiid. It has been shown in other spinose spatangoids, such as *Lovenia*, that such spines afford a degree of protection from cassid predation (McNamara 1994). Another factor could be that spatangoids have a greater range of burrowing spines and consequently burrow at a faster rate than cassiduloids, thereby potentially avoiding attacks (Souto et al. 2023). The remaining four gastropod-predated echinoid species each have only single bored individuals and specimen numbers of four or less (see Table 1), precluding any meaningful assessment of the degree of predation pressure on these taxa.

Of the seven echinoid species that show no evidence of gastropod predation — *Temnocidaris (Stereocidaris) cudmorei, Ortholophus* aff. *bittneri*, *Pleurosalenia tertiaria*, *Fossulaster susae,* ?micrasterid indet., *Protenaster preaustralis* and *S. (Paraster)* cf. *tatei* — *Protenaster, Pleurosalenia*, *Schizaster* and the ?micrasterid indet. are each known only from single specimens, suggesting that this lack of predation may simply reflect a statistical bias. Apart from *Pleurosalenia tertiaria,* which is known from only two specimens, the lack of gastropod predation in the more common *Fossulaster susae* (n=104) and *Ortholophus* aff. *bittneri* (n=16) could be due to their extremely small test size acting as an effective predator avoidance mechanism — with a maximum test length of 5 mm, even the largest *Fossulaster* is likely to have provided minimal nutrient resources for a predatory gastropod.

TABLE 1 Specimen numbers for middle Eocene echinoids from the Nanarup Limestone and Manypeaks limestone. Specimen equivalents are calculated from the number of 'whole' specimens (one), 'partial' specimens (half) and 'fragments' (quarter). These are given after the total number in the format (whole/partial/fragments). The number of bored specimens are presented, and are also expressed as percentages of the total number of specimens and the number of specimen equivalents. * An incomplete incision, representing a failed predation attempt.

Species	Specimens	Spec. equiv.	Bored	Spec. %	Spec. equiv. %
T. (*Stereocidaris*) *cudmorei*	74	*37* (0/74/0)	0	0	0
Ortholophus aff. *bittneri*	16	*8.25* (4/5/7)	0	0	0
Pleurosalenia tertiaria	2	*2* (2/0/0)	0	0	0
Eurhodia westaustraliae	4	*2.5* (1/3/0)	1	25	40
Australanthus longianus	25	*11.5* (1/18/6)	4	16	38
Echinolampas posterocrassa	385	*212* (39/346/0)	44	11	21
Fossulaster susae	104	*72* (43/57/4)	0	0	0
Cyclaster jamiei	4	*2* (0/4/0)	1*	25	50
?*Isaster* sp.	2	*1* (0/2/0)	1	50	100
micrasterid indet.	1	*1* (1/0/0)	0	0	0
Hemiaster (Bolbaster) subidus	2	*1.5* (1/1/0)	1	50	66
S. (*Paraster*) cf. *tatei*	1	*1* (1/0/0)	0	0	0
Protenaster preaustralis	1	*1* (1/0/0)	0	0	0
Gillechinus kaitae	47	*20.25* (4/22/21)	3	6	15

It has been suggested that small body size is a 'crypsis' anti-predation strategy, allowing the potential prey to hide from predators (McNamara 1994, pp. 790–791). However, an alternative explanation could be that at this early stage in the evolutionary history of cassids, these gastropods may not have been adapted to feeding upon such small prey. This is supported by the observation of Ceranka and Złotnik (2003), who noted the presence of cassid predation on very small middle Miocene *Echinocyamus linearis* Capeder, 1906 from Poland. Of comparable size to *Fossulaster susae*, 4% of this Miocene species show evidence of cassid predation. Moreover, Grun et al. (2017) found that about 11% of specimens of *Echinocyamus stellatus* Capeder, 1906 from the Miocene of Malta had been subjected to cassid predation. In their study of the Recent species *Echinocyamus crispus* Nebelsick and Kowalewski (1999) found that more than 70% had been preyed upon by cassids. This suggests an improved adaptation by cassids through the later Paleogene and the Neogene to prey on very small echinoids.

Even though the relatively large cidaroid *Temnocidaris (Stereocidaris) cudmorei* is represented by 74 incomplete tests from the Nanarup and Manypeaks limestones, none show any evidence of cassid predation. The test of this epifaunal echinoid is substantially thicker than that of the burrowing echinoids, which may partly explain the absence of predation on the taxon, with cassids at this time neither having the ability to predate upon cidaroids with thick tests nor to cope with the dense array of large primary spines.

LOCATION OF BOREHOLES

The tendency of gastropod predators to target certain echinoid species and particular areas of the prey's test has been well recorded amongst both living and fossil species (Hughes and Hughes 1981; Gibson and Watson, 1989; McNamara 1994; Grun et al. 2017; Mancosu et al. 2022). Gibson and Watson (1989) considered that areas usually targeted by predators would be those first intercepted — in burrowing species, this would be the aboral surface, specifically the apical and interambulacral areas. Likewise, Mancosu et al. (2022) noted that almost 75% of cassid predatory boreholes in specimens of *Agassizia* from the Miocene of Sardinia occurred on the aboral surface. Of the genera present in the Nanarup and Manypeaks limestones, *Echinolampas, Gillechinus, Hemiaster, Cyclaster, Schizaster* and *Protenaster* would have burrowed to varying degrees, and thus it would be assumed that the aboral surfaces, especially of shallower burrowers like *Echinolampas* and *Gillechinus*, would have been the more common sites attacked, as Grun et al. (2017) noted in gastropod predation on Miocene *Echinocyamus*. However, *Australanthus, Eurhodia, Bolbaster* and ?*Isaster* have most boreholes either ambitally or adorally. *Gillechinus* has one adoral and one aboral, whereas *Echinolampas* has a roughly equal distribution, with adoral incisions slightly more common than aboral ones. This suggests that *Echinolampas* and *Gillechinus* were shallow or even partial burrowers that were more easily attacked in the ambital and adoral parts of the test. This supports the view that *Echinolampas* may have been a suboptimal burrower (McNamara and Philip 1980).

Another, perhaps more significant, factor in borehole placement appears to reflect the distribution, concentration and size of tubercles (and therefore spines) on the prey's test. Boreholes are most commonly developed on those areas of the test where the tubercles are very small, or widely spaced. Conversely, they tend to be less common in areas with dense tubercles, and hence dense spine cover, as dense spine cover is more likely to hinder the gastropod's ability to penetrate the test. Using *Australanthus longianus* as an example, all of the recorded boreholes are preserved on the adoral and ambital regions of the test. Although the largest tubercles, and hence largest spines, occur on the adoral surface in this species, the placement of the boreholes close to and on the ambitus implies attacks centred in areas of smaller tubercles and hence smaller spines. As the anterior aboral surface had smaller spines than in the ambital region, it would be expected that this could have represented an equally good area for boring; however, not a single aboral borehole is known from this part of the test in this species. *Echinolampas posterocrassa* possesses no large tubercles or spines, having been covered in an even covering of fine spines. This may explain the random distribution pattern of the boreholes seen in this species. In *Eurhodia westaustraliae*, like *Australanthus*, the largest tubercles are developed adorally, with the ambital and dorsal regions hosting only fine spines, likely explaining the borehole placement near the ambitus in the single predated specimen.

In *Gillechinus kaitae*, no boreholes occur in the region of the large anterior aboral defensive spines characteristic of this species. Instead, the aboral boreholes occur towards the ambitus, where the spines would have been extremely small, and adorally in the midst of small, widely spaced spines. The boreholes in WAM 07.444 are all situated in the posterior part of the test, away from the location of the primary spines. One is present very close to the periproct. This distribution of incisions is reminiscent of those in *Lovenia forbesii* (Tenison Woods, 1862) from the early Miocene of the Murray Basin in South Australia, which McNamara (1994) attributed to predation in an area of the test not well covered by the aboral primary spines. The relationship of predated areas with tubercle (and thus spine) style suggests that even in the early evolutionary history of cassids, they may have been selective in the area of the test they attacked.

WATER DEPTH AS A CONTROL ON PREDATION

Farrar et al. (2020) and Petsios et al. (2021) have recently shown that the incidence of gastropod drilling of echinoids coincided with the evolutionary expansion of the cassids, which, on the basis of modelling, they consider could have been initiated in the early Eocene and rapidly intensified up to the Oligocene. The absence of *Oichnus simplex* in late Paleocene echinoids, and presence in middle Eocene forms from the western margin of the Australian continent, would tend to support this conclusion, although no early Eocene fossil examples of cassid predation on echinoids have been described to date. Both Farrar et al. (2020) and Petsiois et al. (2021) have questioned the extent to which this rise in predation pressure during the Paleogene contributed to the infaunalisation of echinoids, arguing that '... a significant increase in drilling predation post-dated infaunalization and coincided with the Eocene diversification of the proposed tracemakers, suggesting that cassid predation was unlikely to play a major role in driving echinoid infaunalization.' (Petsios et al. 2021, p. 5). As they point out, the infaunalization that began in the Mesozoic could have equally been driven by the many other organisms that preyed upon echinoids, such as crustaceans or fishes. McNamara (1994) previously argued that patterns of infaunal echinoid evolution toward adaptations to inhabiting finer-grained sediment, often in deeper water, could have been driven, in part, by cassid predation pressure acting on clades at the species level, rather than at higher taxonomic levels. As Petsios et al. (2021) have argued, cassid predation '... may still have contributed to the continued radiation of infaunal echinoid clades, such as clypeasteroids, in the Cenozoic, given the high rates of cassid predation in some modern echinoid populations'.

It has been shown that in modern seas, levels of cassid predation tend to decrease with increasing water depth as the diversity of these gastropods declines (McNamara 1991). It has been suggested that this is the reason for many lineages of echinoids having evolved at the species level into deeper-water niches throughout the Cenozoic (McNamara 1994). If this was the case, then the transition from shallow to deeper water echinoid faunas should correlate with a decrease in the number of cassids, and thus a decrease in the rate of gastropod predation. Such a case has been demonstrated for three species of *Lovenia* from the Miocene of southern Australia (McNamara 1994).

In the case of the Manypeaks limestone, which is coeval with the Nanarup Limestone, it is a somewhat finer-grained, siltier carbonate unit which is likely to have been deposited in deeper water than the bryozoal calcarenite of the Nanarup Limestone. Where the Manypeaks limestone echinoid fauna differs fundamentally from the Nanarup Limestone fauna is that it contains a transitional spatangoid to cassiduloid–echinolampadoid biofacies, unlike the dominantly cassiduloid–echinolampadoid biofacies of the Nanarup Limestone (McNamara and Martin 2022).

In terms of patterns and frequency of cassid gastropod predation, the instances of predation are higher within the Nanarup Limestone, with 8.6% (n=621) having incisions compared with 2.5% (n=40) in the Manypeaks limestone. In terms of specimen numbers, this means that only a single echinoid specimen (*Echinolampas posterocrassa)* in the Manypeaks limestone suffered cassid predation. Such disparate sample sizes would seem to preclude any meaningful comparison of the respective predation levels in the two biofacies. However, *Gillechinus kaitae*, which is known from similar specimen numbers in both limestones (28 in the Nanarup and 19 in the Manypeaks), offers some support for the contention that cassid predation might have been less intense in deeper-water sediments. The *Gillechinus* specimens in the finer-grained Manypeaks limestones show no evidence of cassid predation, whereas three cassid-predated specimens of *Gillechinus* are present in the coarser-grained Nanarup Limestone.

CONCLUSION

The middle Eocene (Bartonian) Nanarup Limestone and Manypeaks limestones of the Esperance Shelf, western Eucla Basin, in southwestern Australia, contain echinoid faunas that provide evidence of the earliest occurrence of cassid gastropod predation on echinoids in Australia, and probably in the world. This is much earlier than the previously reported earliest Australian record, from the upper Oligocene Jan Juc Formation. Their presence in the middle Eocene correlates with the earliest record of cassid gastropods in Australia, in an unnamed middle–upper Eocene unit of the Southern Carnarvon Basin.

Half of the 14 species recorded in these limestones show evidence of cassid predation, with an average rate of predation of 8.2% (*13.9%*). All taxa are irregular echinoids that burrowed in the sediment. Of these, only three species — *Echinolampas posterocrassa, Australanthus longianus* and *Gillechinus kaitae* — have large enough samples to provide meaningful assessment of species-level predation, with *G. kaitae* having the lowest levels at 6% (*15%*), followed by *E. posterocassa* with 11% (*21%*) and *A. longianus* at 16% (*38%*). The spatial distribution of incisions on all taxa shows attacks were on both the adoral and aboral surfaces. The distribution of incisions on *Gillechinus*, a taxon that possessed primary defensive spines, suggests these spines functioned as effective anti-predation structures. Although the proportion of bored echinoids is substantially less in the Manypeaks limestone, with only one specimen found with a cassid gastropod incision compared with 54 in the Nanarup Limestone, the disparity in specimen numbers beween the two limestones precludes any meaningful assessment of the degree to which cassid predation levels vary bathymetrically.

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Buraminya (Cave Rock): an important cultural site in the Ngadju Native Title area, southern Western Australia

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ABSTRACT – Two rock art sites have been recently recorded from the Ngadju Native Title lands of southern Western Australia: Buraminya (Cave Rock) and Cave Hill. Here we present the first published recording of the greater Buraminya site, which has a large repertoire of hand stencils, hand prints, paintings, drawing and scratchings. The use of scratching in southern Western Australia has not been previously documented, nor has the practice (here represented by a single example) of the combining a printed hand within a hand stencil forming a unified composition. Two discrete art periods were identified: an early phase of red hand stencils, and a later phase where media, techniques, colours and motif types became greatly varied. The age of the early phase is unknown but the later phase ceased before dated graffiti was added in 1896. The illustration and quantification of the art at Buraminya now avails its assemblage to be compared with other rock art sites, cultural traditions and regions.

KEYWORDS: Ngadju, rock art, hand stencils and prints, scratching, Buraminya cave.

INTRODUCTION

Rock art is an Aboriginal artefact of cultural practice that occurs throughout Australia. Despite the recording of thousands of rock art sites, particularly over the past 50 years, knowledge of the rock art styles of some areas of the country remains unknown or poorly understood in the public domain. In some cases, this is a decision the Aboriginal communities themselves have made, preferring to keep this knowledge to themselves. In other areas it has been a consequence of little or no archaeological study. The Ngadju Native Title determination area, around Norseman in southern Western Australia, contains two rock art sites: Buraminya (Cave Rock) and Cave Hill. The location of Cave Hill is well known to the public, whereas that of Buraminya is restricted for security reasons.

In 2023, the Ngadju Conservation Aboriginal Corporation commissioned the detailed recording of the Buraminya (Cave Rock) and Cave Hill sites, both of which are within their Ngadju Native Title area (Figures 1–2). Here we present a summary recording of Buraminya, the larger of the two rock art sites, with nearly 300 varied, although mostly weathered, motifs. Detailed description, tabulation, and full illustrations of the art for both sites are included in reports held by Ngadju Conservation Aboriginal Corporation (Gunn 2023a, 2023b). Indigenous Culture and Intellectual Property Copyright rests with the Ngadju people, and the images cannot be reproduced without the permission of the authors.

In a State-wide review of Aboriginal rock art, Davidson (1952) did not record any art sites from Ngadju country, but extrapolation from sites within his Southern and South-Central art areas, suggests the dominant form of art throughout the region would be hand stencils. More recent studies of Nyunga rock art (within Davidson's Southern Area), to the immediate west of Ngadju country, have found in addition to hand stencils, simple and complex linear (striped) designs also occur as a notable component of the region's pigment repertoire (Gunn et al. 2017).

Buraminya is within an isolated area of the Dundas Nature Reserve, and is little impacted by the public. The less-decorated site at Cave Hill, in contrast, is within the Cave Hill Nature Reserve; a reserve widely publicised to the general public and with limited management structures to supervise visitor movements at the site (e.g. Australia's Golden Outback n.d.; Parks and Wildlife Service 2014).

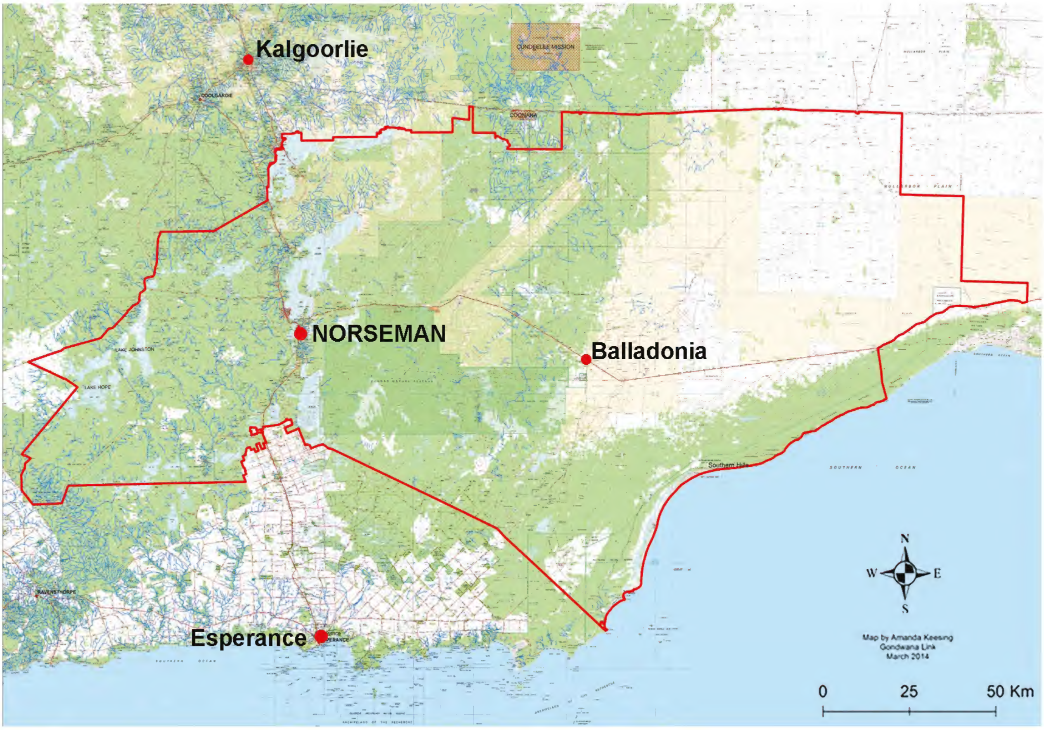

FIGURE 1 Location of the Ngadju Native Title area.

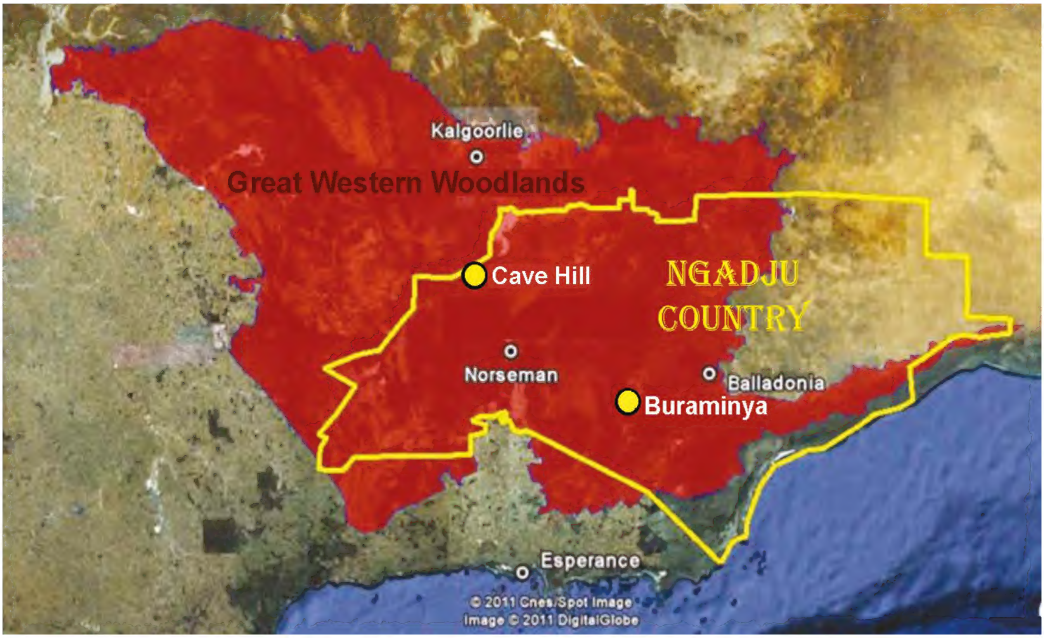

FIGURE 2 The Great Western Woodlands (red) with an overlay of the Ngadju Native Title area and the two Ngadju rock art sites; Buraminya and Cave Hill.

THE ENVIRONMENT OF NGADJU COUNTRY

A significant part of Ngadju land is situated within the Great Western Woodlands (GWW), a temperate and semi-arid eucalypt woodland (Horton 1994; Gondwana Link 2024). The GWW is biologically diverse with over 3,000 flowering plant species and over 300 faunal species (Watson et al 2008, n.d.). The area is on the southern margin of Australia's Arid Zone, but the climate is Mediterranean: hot, dry summers and cool, wet winters, with an annual rainfall of around 288 mm (BOM 2023). The geology around the two shelters consists of remnant inselbergs surrounded by broad sandplains overlying lateritic duricrust, with scattered low granite outcrops and pavements, and low ridges of greenstone (Hunter 1991). There is little standing water in the region as evaporation rapidly dries out the few claypans and large salt lakes (2200 mm/yr; BOM 2006) far exceeds rainfall (Hunter 1991: 4). The gnammas (rock holes: Twidale and Corbin 1963) on inselbergs and pans on rock-pavement, however, provide a valuable if impermanent reserve of fresh water. The rain runoff from the inselbergs also supports a fringe of lush vegetation around the base of the domes. These factors thus established inselbergs as essential navigational landmarks with both food and water resources for Aboriginal people (Bindon 1997; Smith 1993 discussed in Rossi 2020; Bayly 1999; Webb and Gunn 2004). These water reserves were also of value to early European explorers, who otherwise found water and feed for their horses scarce throughout the region (e.g. J.S. Roe in 1852 discussed in Bowdler et al. 1989), and for sandalwood-cutters who relied upon the water they found in 'granite rockholes' (Bowdler et al. 1989). Gnammas have been reported seven kilometres to the south of Buraminya, and these are thought likely to hold water throughout the summer months (Corsini 1993).

METHODS

Aboriginal rock art contains essential information about the individuals and society at the time that it was produced. In most areas of Australia, the tradition of rock art production is no longer continued and what remains is deteriorating through the effects of natural weathering and human interference. It is now generally recognised that the detailed recording of Aboriginal rock art is an essential step before any research, conservation, or management action can be undertaken. This is particularly pertinent, as any of these actions may lead to the destruction of the motifs under study (Loubser 1997: 14). All motifs and fragments need to be recorded to document the status of the existing art content and the context of the motifs at a site. The resultant graphic record then forms a baseline document for monitoring both during and following any subsequent studies. Adequate recording requires intensive observation of both the rock surface and the technical aspects in the field. Also, all recordings must make use of at least two methods (sketching, schematic diagrams, photography, DStretch image enhancement programme, photo-tracing, 3D modelling, etc), selected according to the nature of the artwork, its environment and the nature of the proposed study (see Rosenfeld 1977; Clegg 1991; Gunn 1995a, 1995b; Heyd and Clegg 2005; Harman 2008, 2015; Gunn et al. 2010; Grussenmeyer et al. 2015; Jaillet et al. 2017). The use of at least two recording methods is to provide the recorder with a clearer appreciation of the art that is being recorded.

The labels given to motif types in the art by the recorder are archaeological terms and do not necessarily reflect the interpretation signified by the motif to the artist. As with all visual art, the true meaning can only be revealed by the artist or someone entrenched within the cultural system the artist came from. Motif types here are referenced to what they appear to the recorder. Motifs with no recognisable shape are classed as either 'simple design' or 'complex design' on the basis of graphic construction, although designs with a 'branched' pattern were recorded as a distinct class of simple design as they are a notable feature in the art here. Colour, technique, form and size (were possible) were also recorded for each motif.

A case for the distinction of preform motifs as art as against freeform motifs as 'marks' has been strongly made by both Rosenfeld (1999) and, from a slightly different angle, Dobrez (2013). Rosenfeld, following Forge (1991), argued that while the act of hand stencilling (or printing) was cultural, the stencil itself was not cultural as it was devoid of style or 'cultural translation' (Rosenfeld 1999: 30). Dobrez, from a psychological view, sees the act of hand stencilling (or printing) and the image as a 'quasi-representational iconic character' that is immediately recognised as a hand, but the image is not an iconic image and that they have 'have the special quality of directly replicating the hand that made them' (Dobrez 2013: 277). While avoiding the reason for the difference, we prefer to follow the archaeological classification of Leslie Maynard (1976) who divided pigment art as either 'mechanical', where the form of the image was dictated by the technique, or 'delineated', where the form of the motif is independent of the technique (Maynard 1977: 391).

Digital photography was the principal recording method used. Photographs were taken with a Nikon 610 full-frame digital camera, with flash and a variety of lens, supplemented by an iPad with the image enhancement DStretch program installed. The use of DStretch was invaluable in recording the art here due to the faintness of many of the motifs. Art panels were distinguished by physical breaks in the rock surface that separated motif clusters. Art panel measurements were taken with a commercial digital laser measurer, with data and observations recorded in a field notebook. The site plan was produced from aerial photographs (Google Earth) and fieldnotes of measurements. Art panels were measured width × length, and the longest measurement of each motif was recorded. For hand stencils and prints the length of the middle finger where possible, or knuckle width if not, were measured to the nearest 0.5 cm (cf. Gunn 2006a).

Fieldwork was undertaken on the 10 March 2023 with the assistance of Ropafadzo Moyo, Leslie Schultz, and Ngadju Rangers Darius Wicker-Evans, Allan Harris, Vicki Graham and Anslem Rex.

The photographs were later run through a more detailed DStretch program and, for clarity of individual motifs, tracings of the art were done in Adobe Photoshop using various layers of DStretch images across the primary photograph. Measurements of individual motifs were taken from the scaled photographs or as measured by Corsini (1993). Due to the irregular form of the surfaces, many measurements of the larger motifs are either approximate or were unable to be measured given the lack of any degree of confidence.

BURAMINYA (CAVE ROCK)

The site had previously been only briefly recorded for the State Site Register as Site 2874 (Corsini 1993). Corsini's report illustrated 47 motifs, noting there were others not recorded. The report concluded that the interior walls were deteriorating and warned that future damage to the art was inevitable.

Cave Rock and its related outcrops are composed of a leucocratic (white) granite, the main block of which is 200 m × 300 m in area and rises to 284 m above sea level, or some 15 m above the surrounding woodland plain (Geological Survey of Western Australia 1988). Within a local woodland of tall eucalypts, the outcrop is not an obvious feature but, situated on the crest of a rise,

FIGURE 3 Buraminya rock art shelter from the north (top), A and B are the western and eastern alcove respectively; profile of the western alcove from the east (bottom), note the human figure scale.

it is notable from a distance. From on top an extensive panorama is gained of the country to the north.

Cave Rock houses a single art site — the large and dramatic Buraminya (Cave Rock) art shelter (here abbreviated to Buraminya). The shelter forms a broad arc 30 m wide and a maximum height of 5m and has a maximum depth of 14 m (Figures 3–4). Both the depth and height vary considerable across the shelter because of its irregular plan and sloping floor. A change in floor level and orientation effectively divides the shelter into two adjoining alcoves:

- Western alcove: a large and commodious bay some 20 m wide, 15 m deep, and 5 m high.
- Eastern alcove: a smaller recess, c. 15 m wide, 10 m deep, and 2 m high. Owing to a low bellying ceiling and rising floor level, however, the useful area for people is effectively limited to the outer five meters of the eastern alcove.

Art occurs on 19 art panels across both alcoves, with the majority occurring in the larger and more open western alcove. The most visually prominent art occurs on Art Panel A, on the western wall (Figure 5). This art panel is immediately inside the shelter at the most convenient entry point to the site as coming from the base of the outcrop. At this point the wall is vertical and well-lit by natural daylight (see below).

The shelter has formed through horizontal erosion, presumably into a layer of weaker rock, undercutting the harder surface layer of the outcrop (see Twidale 1980: 109–123). At the western end of the shelter, the lip of overhang is around two-metres thick. At the eastern end, a section has already broken away along a joint or fault line in the bedrock, forming a pile of large blocks at the mouth. The fault or joint continues through the remaining ceiling of the western alcove and western wall of the shelter. This weakness will, most likely in time, cause a similar collapse of the western ceiling, destroying some of the ceiling art and exposing the western wall and its art to the elements. The timing of the collapse cannot be predicted, but, as the erosion process is still active, the shelter will continue to deepen, eventually causing the outer overhanging ceiling to collapse under its own weight. Otherwise, the interior shelter is generally stable, but small areas of exfoliation and granular disintegration are apparent, including areas that contain art, and where it has partially, or in one location amid other art most likely fully, destroyed a quantity of the art.

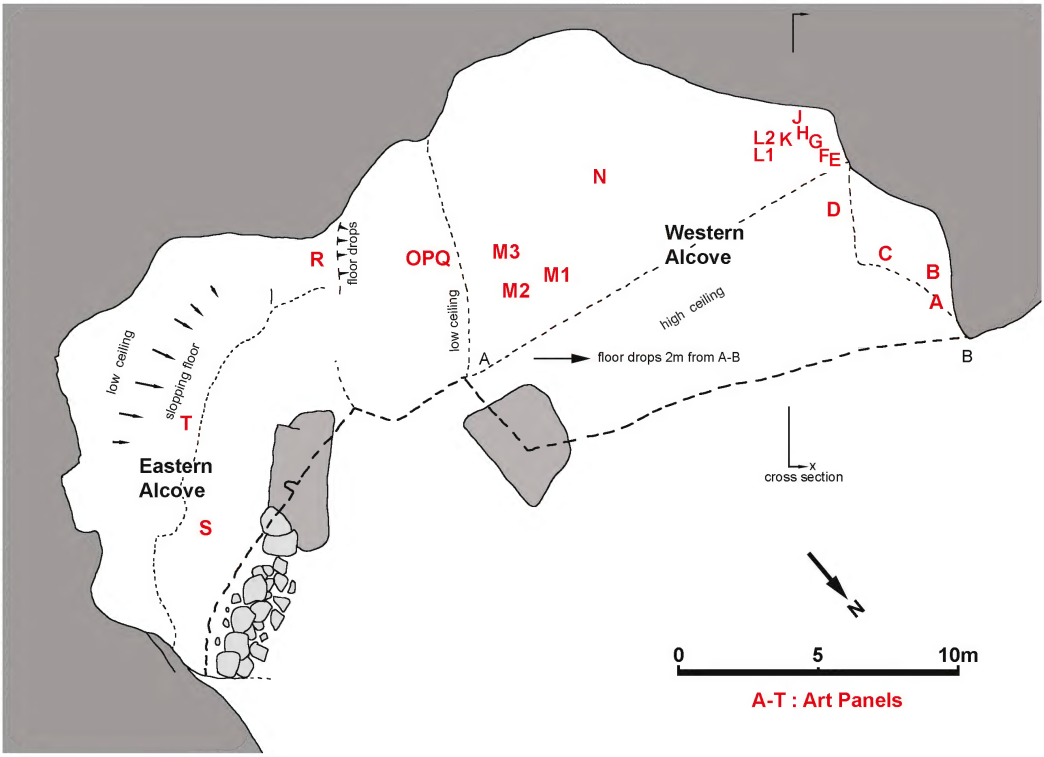

FIGURE 4 Plan of the Buraminya shelter showing the location of the 19 art panels (Art Panels L and M were subdivided for the convenience of recording).

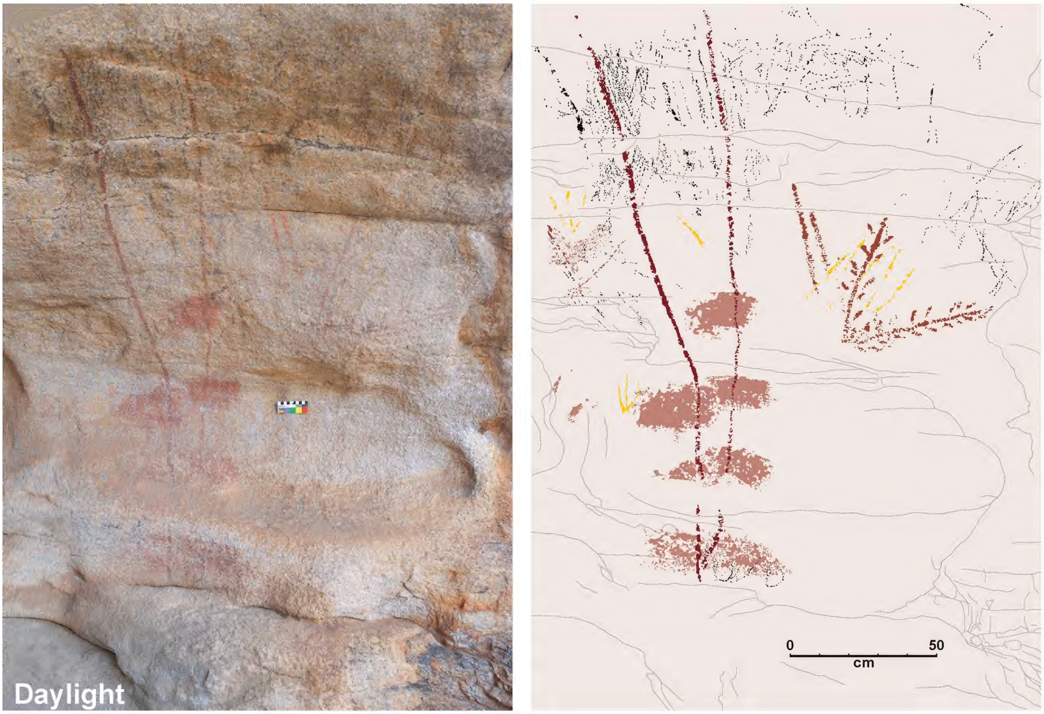

FIGURE 5 Photograph and photo-tracing of Art Panel A involving paintings (red and yellow) and drawings (red and black).

The floor of the shelter is sloping but relatively flat, with a light soil cover over bedrock, indicative of a low excavation potential. No surface artefacts were noticed within the shelter or on the frontal talus. Similarly, there are no signs of manual manipulation or modification of the interior of the site. No survey has been undertaken around the shelter, but a random stop at two bare rock pavements, a kilometre or so to the north, revealed light scatters of stone artefacts over most of the exposed areas.

THE ART OF BURAMINYA

The art within the cave is generally very weathered but, on entering, the immediate impression is of a few, long vertical lines in red, and three solid ovoids also in red on the western wall by the natural ‘entrance’. Much of the art is difficult to see because of the deteriorated pigments and due to the dark interior of the site.

In total, 277 individual marks (motifs) in various techniques were recorded: 92 drawings, 81 hand stencils, 59 hand prints, 41 paintings, three scratchings, and one pigment fragment of unclear technique. These motifs occur on 19 art panels scattered throughout the shelter (Art Panels A–T; Figure 4 — there is no Art Panel I due to similarity with the numeral 1). The art panels within the shelter occur in four spatial groups: Art Panels A–L on the western wall of the Western Alcove, Art Panels M and N on the central ceiling, and Art Panels O–R within a small confined recess at the upper eastern end. Art Panels S and T are on the outer wall and interior ceiling of the Eastern Alcove. The art panels range from large (Art Panel M, 9.0 m^2) to very small (Art Panel D, 0.1 m^2), and the number of motifs per art panel range from 2 to 45, with a trend towards a positive correlation between art panel size and motif numbers (Figure 6). While Art Panels L and Q have notably few motifs per metre than the others, no art panels have excessively high numbers of motifs. This suggests that the artists preferred to keep their art uncluttered rather than undertake intensive superpositioning, such as is evident in areas of northern Australia where rock art production was higher (Kimberley, Arnhem Land, and Cape York). At Buraminya, however, most of the rock panels suitable for rock art application were utilised.

The art was produced using five different techniques and four different colours (Table 1), although within these classes several hues can occur. Red stencils are the most common colour/technique combination, and red is the only colour used by all four additive (pictogram) techniques. Black (charcoal?) pigment only occurs as drawings and the four interpreted orange motifs are all prints. Scratching is a subtractive (petroglyph) technique and the unpatinated state of the scratchings indicates

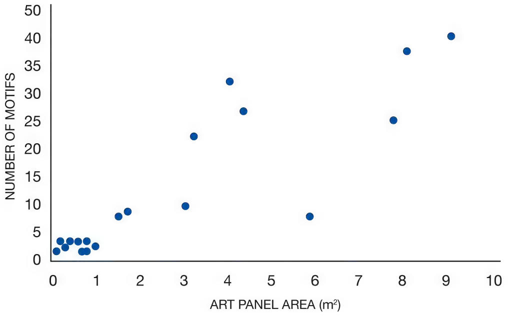

FIGURE 6 Plot of motif numbers by Art Panel area.

they have weathered little since they were produced. These only occur on the outer wall of the Eastern Alcove (Art Panel S). Drawings are restricted to art panels on the western wall (Art Panels A–F, H and J) with the exception of four small motifs that occur on Art Panels Q and R that will be discussed further below.

Stencils occur on all art panels except Art Panels A, D–F, and T; most of which are hand stencils (Figure 7). Art Panels B and H each have 16 tightly concentrated groups of stencils. Of the panels without hand stencils, Panels D–F and T are small, Art Panel A is large and prominent.

Paintings is the most widespread technique in the shelter, occurring in small numbers throughout the shelter (Art Panels A–F, H, M, O and T). Paintings are, however, numerically far more common on the western wall art panels.

Prints (all of which are hand prints) occur on Art Panels G–H, K–M. This cluster forms an arc over the ceiling of the western alcove, with the greater majority (88%) on the higher ceiling Art Panels L–M (Figure 8). Hand prints are heavily concentrated on the adjacent ceiling Art Panels L–M (53 of the 60 prints); two of the largest art panels in the shelter (7.7 m^2 and 9.0 m^2 respectively).

Of the five colours used, red is the most widespread, occurring on all art panels except Art Panel K. Fifty-one of the 59 black motifs occur together on the western wall (Art Panels A–C). Yellow drawings only occur on Art Panels A (n=4) and B (n=5), while Art Panels G–H each contain a single yellow hand stencil. All other hand stencils are in red, as are all but four of the hand prints. The exceptional hand prints consist of four in orange: three on Art Panel K and one on Art Panel H. The other orange motif (fragment), whose technique cannot now be interpreted, was most likely also a hand print as it also occurs on Art Panel K close to the other orange hand prints.

MOTIF TYPES

Altogether 30 different motif types were distinguished, including 24 freeform types and six preform types, and another amorphous category of fragments (weathered remnants to which no particular motif type could be assigned (Table 2). Freeform motifs, such as with drawing and painting, are graphic elements that are not restricted by their technique. The shape of Preform motifs, in contrast, is determined by their techniques, such as with hand or object stencils and prints.

THE FREEFORM MOTIFS

The most common freeform motif type at Buraminya is the line. Lines are here defined as relatively straight, singular marks (as opposed to pairs or sets of Lines), of any length (from 5 cm to 520 cm in length), colour, or orientation (from horizontal to vertical). Lines are the dominant motif type in both drawings and paintings (54% and 25% respectively) (Table 2). The longer lines are amongst the most visually apparent freeform motifs in the shelter. No other motif type is represented with unusually high numbers. The range of motif types by technique largely reflects the number of motifs present: drawing 17 motif types with 70 motifs, painting 12 motif types with 28 motifs, and scratching with three motifs

TABLE 1 Motif colour by technique (*technique of one motif is unclear and is not included).

Colour	Draw	Stencil	Print	Paint	Scratch	Total
Black	59					59
Red	24	82	55	32		193
Yellow	9	7		1		17
Orange			4			4*
Unpatinated					3	3
Total	**92**	**89**	**59**	**33**	**3**	**276***

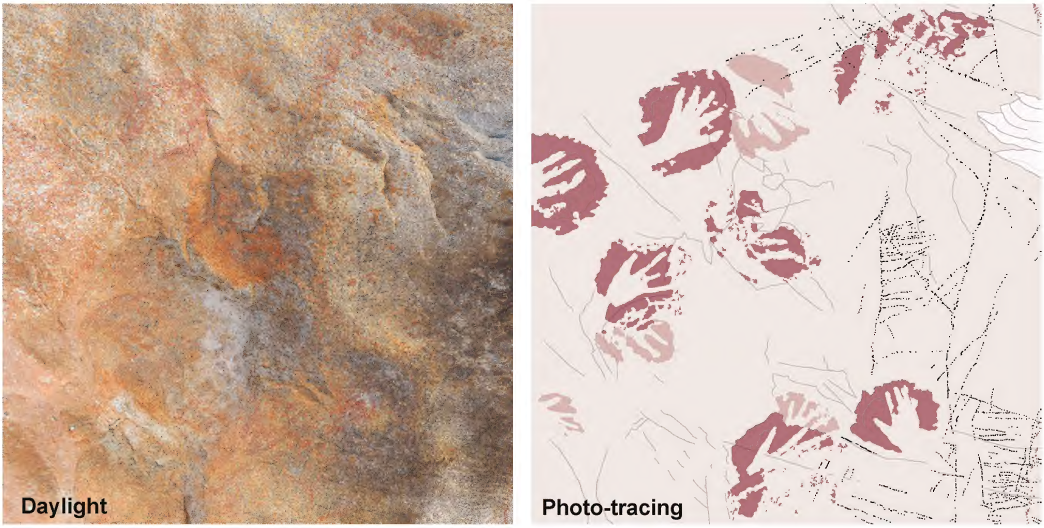

FIGURE 7 Hand stencils and charcoal drawings on Art Panel B3.

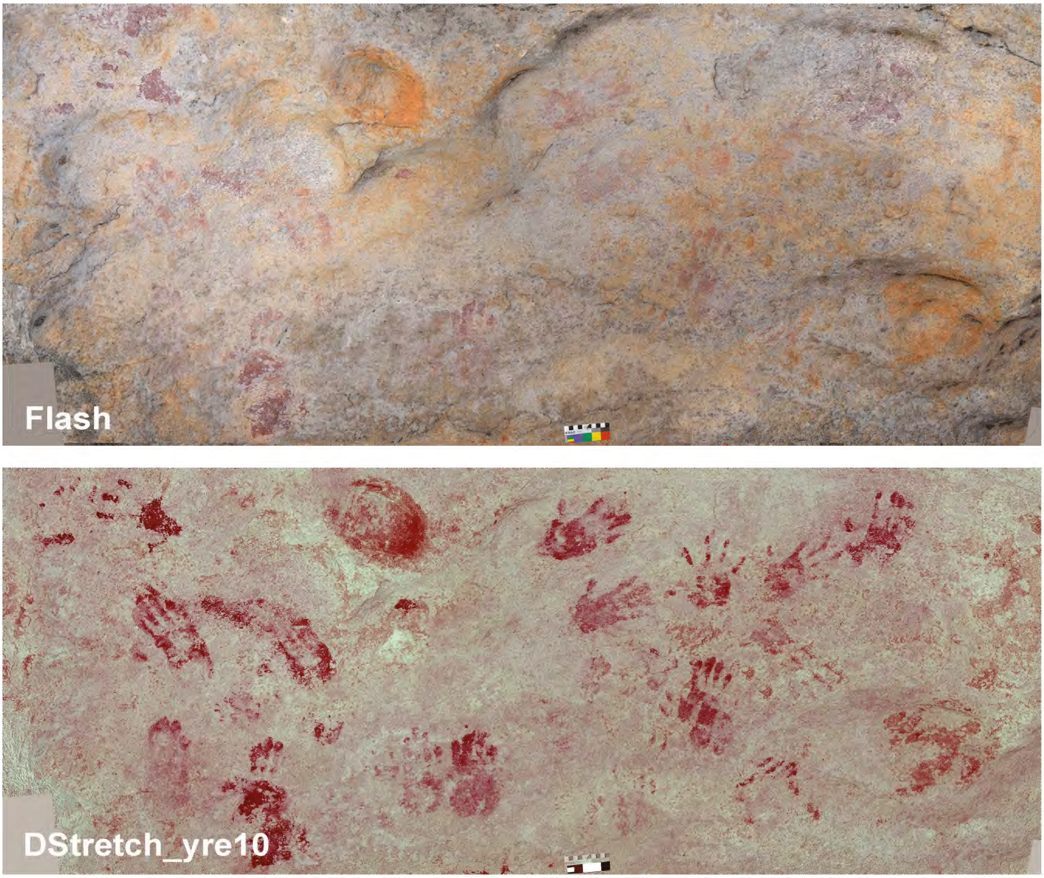

FIGURE 8 Hand prints and smears on Art Panel L2.

each of which is a different motif type. Only two motif types were produced in each of the three techniques: simple design and branched design (a specialised form of simple design; Figure 9A).

Only three of the 22 freeform motif types are recognisable shapes: bird tracks (8), macropod tracks (2) and snake (Figure 9B–C). Together these account for 11% of the repertoire. Two types of bird track motifs occur: three-toed and four-toed types. While often recorded as emu and crow tracks respectively, there is no reason why they could both not represent a range of other bird types represented with in the Ngadju environment. A single example of a what is likely to represent a walking bird is shown by the representation of a trail of bird tracks (Figure 9B). Such trails require verbal accompaniment to elaborate a story that develops over time (cf. Munn 1973: 123–124)

Similarly, while macropod tracks are traditionally considered to represent a kangaroo (regional species assumed), they could equally equate with the tracks of any of the macropod species (Figure 9B).

The snake motif was identified by its regularly undulating body shape (Figure 9C). Although apparently in outline, the outline form is incomplete and the impression of a whole body derives from a visual allusion. The snake drawing has been intentionally placed horizontally over (superimposed on) an earlier hand stencil. Above and below the Snake motif are two horizontal undulating lines (both of which, like the snake motif, are superimposed over earlier hand stencils. The two undulating lines are therefore most likely to be simplified forms of the snake motif. These three drawings occur close together within the dark, secretive recess at the eastern end of the Western

TABLE 2 Freeform motif type numbers by technique.

Motif type	Drawing	Painting	Scratching	Total
Straight line	38	7		*45*
Bar row	8			*8*
Simple design	3	2	1	*6*
Bird track 3-toed	2	4		*6*
Ovoid	1	4		*5*
Aggregate	4			*4*
Branched design	1	1	1	*3*
Straight line pair	2	1		*3*
Hand smear		3		*3*
Bird track 4-toed	1	1		*2*
Curved line	2			*2*
Undulating line	2			*2*
Macropod track		2		*2*
Complex design		1	1	*2*
Bird track trail		1		*1*
Dot		1		*1*
Bar	1			*1*
Bar pair	1			*1*
Barred oval	1			*1*
Snake	1			*1*
Straight line set	1			*1*
V-shape	1			*1*
Total	**70**	**28**	**3**	**101**
Fragments	22	8	0	30

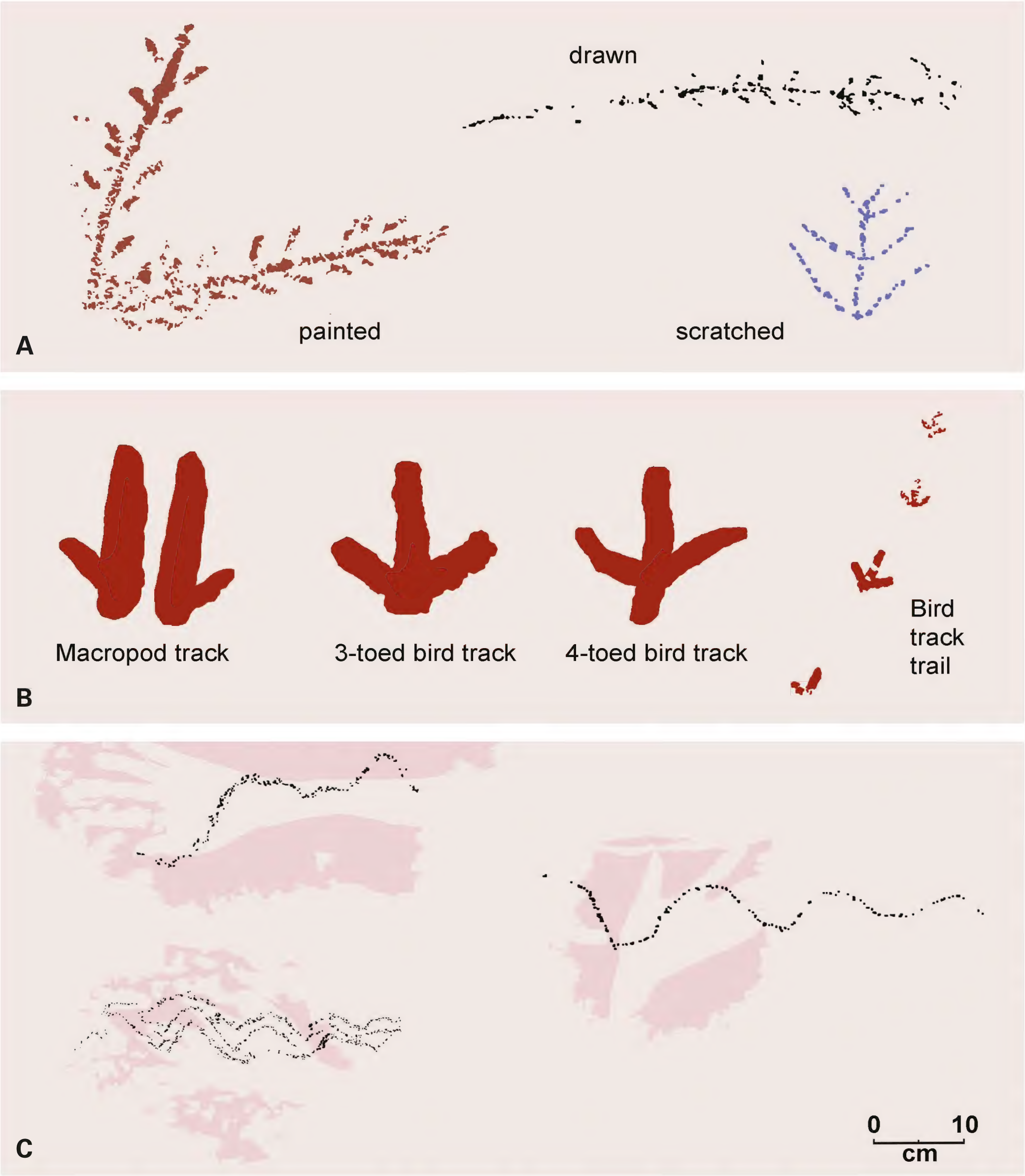

FIGURE 9 A) Branched design represented in each of the three freeform techniques; B) painted examples of stylised fauna track motifs; C) three charcoal 'snakes' drawn over hand stencils.

Alcove on Art Panels P and Q. Given their similar technique, colour, and state of preservation, it can be assumed that the three drawings, as well as an associated charcoal line, were produced by the same artist. Further, the deliberate association of the snake forms and the hand stencils implies that their visual association/composition had a particular meaning for the artist of the drawings.

Each of the three scratching are very faint freeform motifs and all on Art Panel S (Figure 10). While scratched motifs have been recorded in the Kimberley (O'Connor et al. 2013; Goldhahn et al. 2023) and Dampier Archipelago (Vinnicombe 2002; Gunn 2007a; Mulvaney 2015), the technique for art has not previously been recorded in the southern part of Western Australia. O'Connor et al. consider scratching in the Kimberley

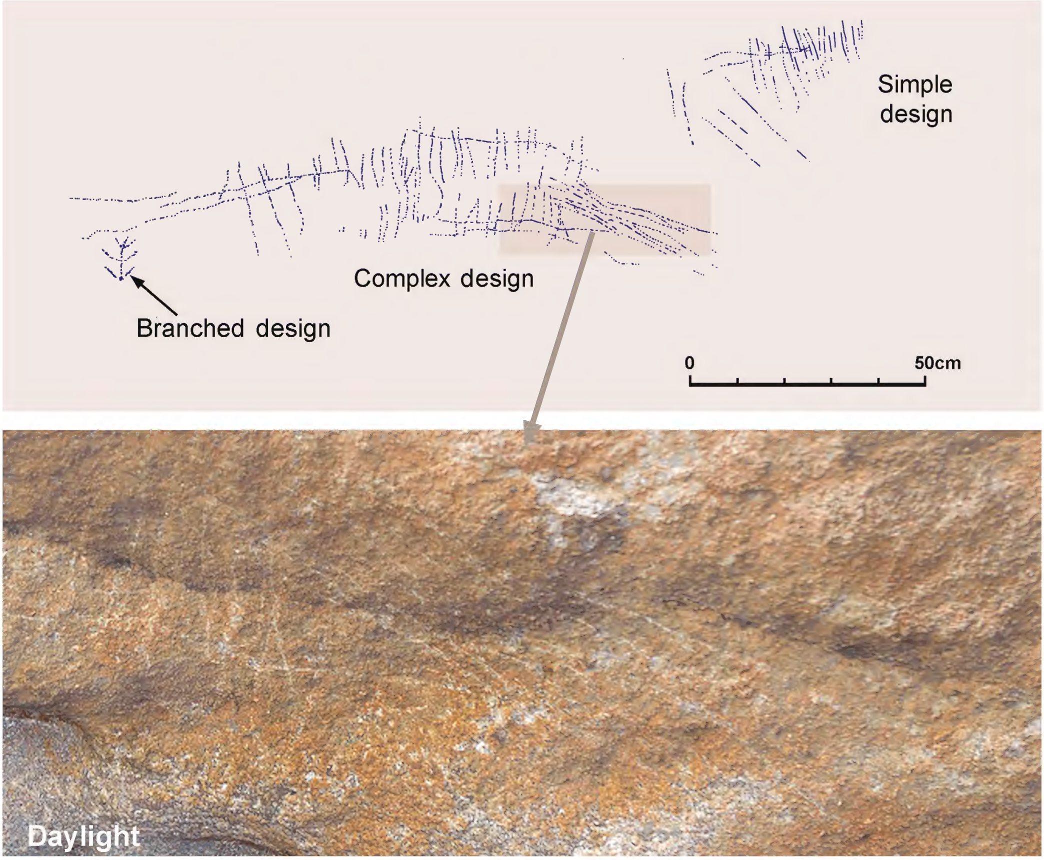

FIGURE 10 The three scratched motifs on Art Panel S and photographic detail of the complex design motif.

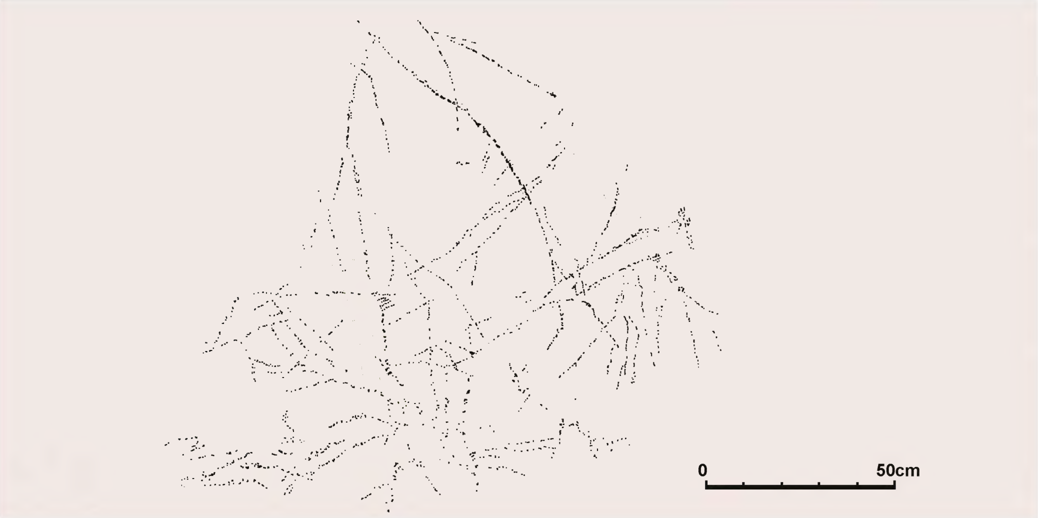

FIGURE 11 Line aggregate (Motif 46) drawn in black on Art Panel B.

to have been produced with a metal object and date to the contact period (station time). The thinness of the scratched lines at Buraminya also appear to have been made with a metal implement (cf. Spry et al. 2002)

The drawn motifs, while being the most numerous, are often some of the hardest to see, and many are discontinuous, in some cases making clear identification of the motif type subjective and size approximate or unreliable (Figure 5). Where a great number of lines or line sets are closely positioned, it was not possible to determine individual motifs. Consequently clusters of drawn line motifs were recorded as an 'aggregate' motif (Figure 11). In some cases these aggregates also include fine black lines of biotite within the bedrock and distinguishing between the drawn and the natural lines becomes tenuous.

In addition to the aggregate motifs, one of the large simple design motifs (Motif 37; Figure 12) has been developed as a composite in four stages:

- An initial drawing in yellow of simple design (a pair of lines that converge at their upper apex; Motif 37b).
- A later red drawn line (Motif 37a) was placed to the left of Motif 37b.
- A second red line (Motif 37d) was affixed to the top of Motif 37a and drawn down superimposing the right side of the yellow motif (Motif 37b).
- A third red line (Motif 37c) was added superimposing the left side of Motif 37b.

A further dark red line (recorded as a separate motif, Motif 34) runs down the right side of Motif 37, and although it follows closely the shape of Motif 37, it is unclear whether it pre- or post-dated it.

The sizes of 76 freeform motifs were able to be measured, although the motifs greater than 200 cm were approximated on account of the undulating surface on which they were placed. Of the measured motifs, 66 are less than 86 cm in length, the other ten range from 139 cm to c. 520 cm. The larger motifs consist of five red drawn lines (c. 200 cm to c. 520 cm), three painted red lines (192 cm to c. 230cm), a yellow drawn simple design (c. 450 cm), and a scratched complex design (139 cm). All are on vertical surfaces: two on Art Panel A, five on Art Panel B, two on Art Panel C, and the scratched complex design on Art Panel S. It is the large motifs on Art Panels A–C (Figures 6 and 12) that give the visual character to the art at Buraminya.

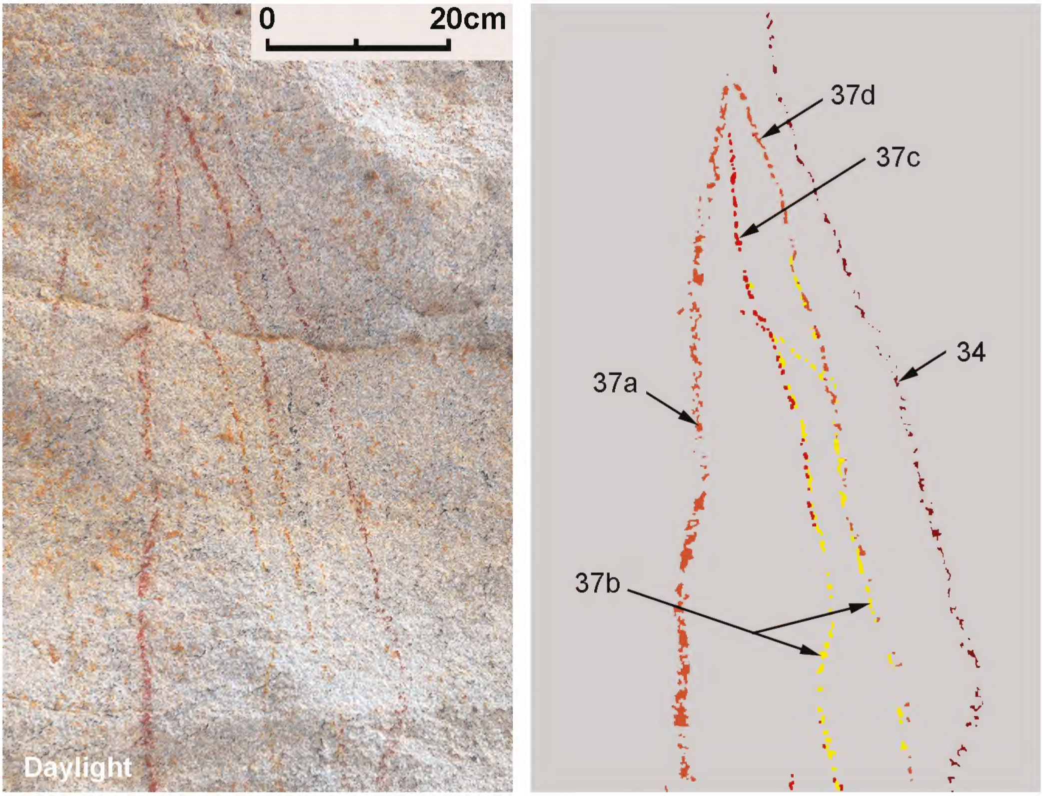

FIGURE 12 Composite simple design (motif 37) on Art Panel B showing different coloured component motifs.

Excluding the ten large motifs, the drawings range from 5 cm to 80 cm in length (median 17 cm), the paintings range from 4 cm to 85 cm (median 16 cm), while the three scratchings are 11 cm, 43 cm, and 139 cm respectively.

Overall then, the repertoire of freeform motifs here is non-figurative and, apart from the single complex design, the graphic structure of the motifs is very simple in form. Simple design and branched design are the only motif types to be produced in all three techniques, but the correspondence between the other motifs of the three techniques suggests they derive from a common art tradition: a tradition that, judging by the good preservation of the freeform motifs are of similar, and not great, age (see below).

PREFORM MOTIFS

The preform motifs here, with the exception of a single object stencil, are restricted to hand stencils and hand prints. The stencils are predominantly of left hands (59% of 68) and the prints are predominantly of right hands (90% of 30), suggesting a population dominated by right-handed people, as right-handed people tend to favour stencilling the left hand and printing with the right-hand (cf. Gunn 2007b). The distinction amongst the stencils, is not as skewed to the majority hand as would be expected from other studies in Australia (e.g. Gunn 2006a) and the 41% of right-hand stencils here implies a greater proportion of left-handed stencillors amongst the Ngadju than suggested by the ethnographic studies in this area by Birdsell in 1938–1939 (Birdsell 1993).

The object stencil is that of a boomerang on Art Panel S (Figure 13). (This may have initially been a pair of boomerangs, but the lower 'possible boomerang' cannot not be clearly defined). This is the only object stencil within the shelter and, although not a complete stencil (being held by the stencillors hand at the right end), it appears to be the common type of symmetrical, returning boomerang.

The two preform motif types found at Buraminya are hand stencils and hand prints, and two examples of printed dots (presumably printed using the finger-tips).

Fourteen 'Variant' hands (Walsh 1979; Wright 1985; Gunn 1998) were recorded in two forms: termed here as Variant V1 and Variant V2. Variant V1 occurs only as hand stencils and Variant V2 only as hand prints (Figure 14). Variant hand stencils and prints are those that vary in the arrangement of the digits from the standard hand stencil or print, where the digits are all splayed fan-like. All Variants were produced with red pigment. Four of the five Variant V1 stencils were produced using the left hand, the other a right hand. The measured Variant V1 hand stencils are all left hands with knuckle widths of 7.0, 7.0, 8.0 and 8.0cm respectively. The Variant V2 prints consist of two left and two right hands, and two whose hand could not be determined. The knuckle widths of the measured Variant V2 hands are 7.0, 10.5 and 11.0 cm. The two prints with knuckle widths greater than 10cm must be of adult men (see below).

An unusual composition on Art Panel G consists of a red hand print (Motif 120) placed fully within an earlier yellow hand stencil (Motif 119). While the pigment covered most of the printed hand, the finger and thumb were pressed on with greater force than the palm, giving what at first glance looks like fingernail on the thumb and fingers (Figure 15). The only other example of 'hand-with-fingernails' known in Australian Aboriginal rock art occurs at Willi Gully, near Horrocks, 900 km to the north-west (Dobrez 2014: 376; pers. obs. 1984). Unlike the example here, however, from poor quality

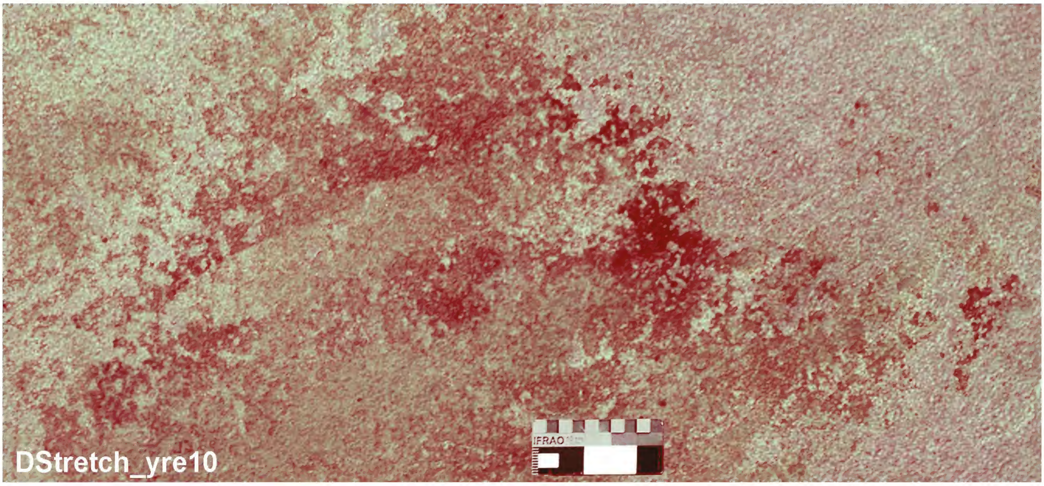

FIGURE 13 Enhanced image of the Boomerang stencil.

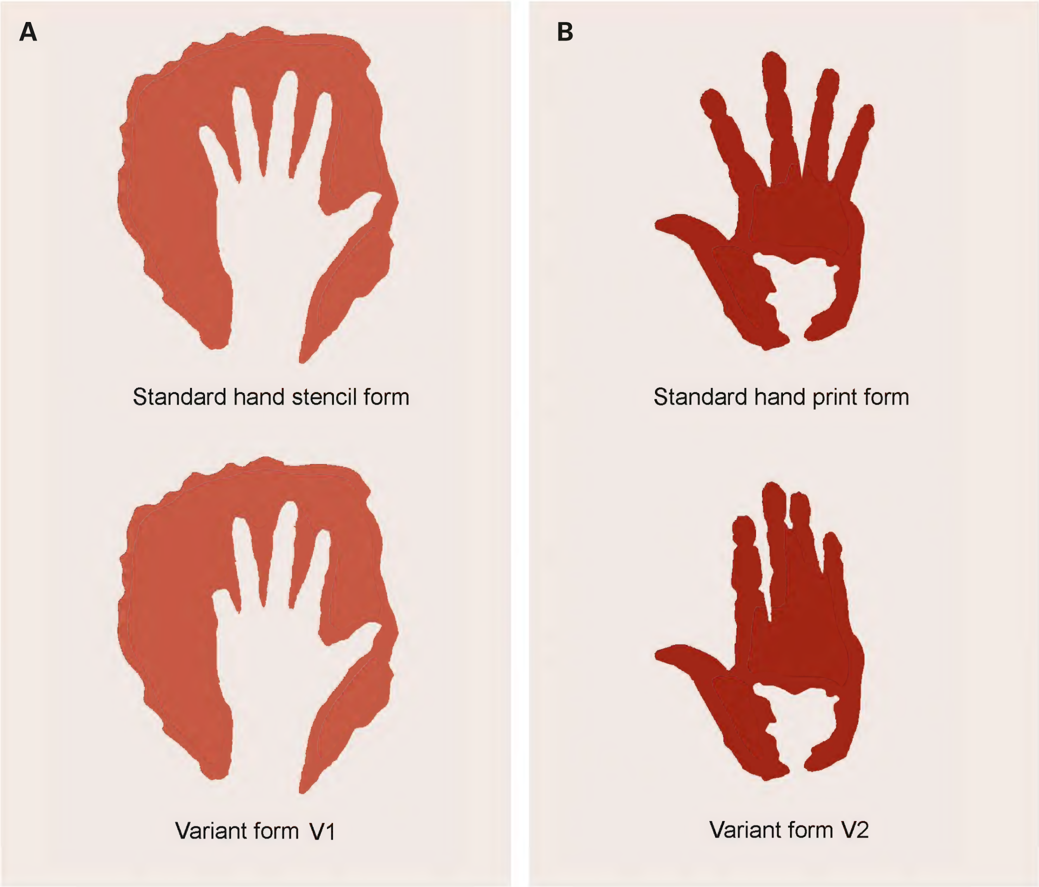

FIGURE 14 The two 'Variant' form hand types: A) Left-hand stencil Variant V1 with little finger truncated; B) right-hand print Variant V2 with fingers closed together.

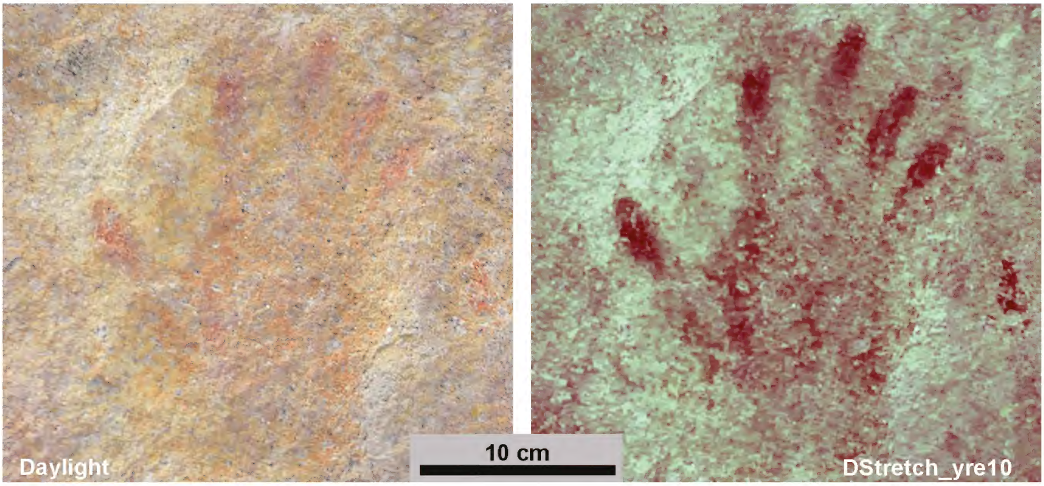

FIGURE 15 Yellow hand stencil carefully superimposed with a red hand print.

TABLE 3 Hand size by technique and age (after Gunn 2006a). Range ±2sd (95% confidence). Any measurement for stencils >8.5 cm and any prints >7.5 cm can be assumed to be of adult males.

Technique	Age range (yrs)	Size range (cm)	Mean (cm)
Stencils	4–6 (infants)	4.5–6.5	5.5
	7–12 (children)	5.5–7.5	6.5
	13–15 (adolescents)	6.5–8.5	7.5
	>15 (adult female)	6.5–8.5	7.5
	>15 (adult male)	7.5–8.5	8.0
Prints	4–6 (infants)	3.5–5.5	4.5
	7–12 (children)	4.5–6.5	5.5
	13–15 (adolescents)	5.5–7.5	6.5
	>15 (adult female)	5.5–7.5	6.5
	>15 (adult male)	6.5–7.5	7.0

TABLE 4 Hand sizes frequencies for stencils and prints.

Knuckle size Class (cm)	Hand Stencils	Hand Prints
5.5	1	
6.0		1
6.5	9	2
7.0	8	
7.5	9	7
8.0	4	1
8.5	7	12
9.0	3	
9.5	2	1
10.0		
10.5	1	1
11.0		1
11.5		1
(n)	***44***	***27***

photographs, the finger-tips of the Willi Gully example appear to have been painted rather than printed.

It has been demonstrated that the sizes of the middle finger or knuckle of the hands can give an approximate age of the person whose hand was printed or stencilled (Table 2; Gunn 2006a). As stencils tend to be slightly larger than the hand stencilled and prints slightly smaller than the hand printed, measurement of 44 of the stencils and 27 of the prints here suggest that the hand stencils contain at least one of a large infant or child, and 12 adult men (Table 3–6). The other 30 hand stencils could represent the presence of large children, adolescents or adult women. Among the hand prints, there are at least 16 adult men, but of the others there is no certainty. Although adult males dominate both techniques, as all age classes are represented it can be assumed that all members of the society are represented, both in the earlier hand stencils and later hand prints. Whether these were all males, or males and females, however, is not shown by the art, as children could have been accompanied by either men and/or women.

Stencils occur throughout the shelter, with minor peaks on Art Panels B, H and L. Art Panel A is the only large art panel without stencils. In contrast, prints are limited to art panels across the ceiling of the main alcove. Art Panel M, that with the highest number of hand prints, is around 2.5 m above the floor and the highest situated art panel.

The greatest range of freeform motif types occurs Art Panels A–C, the prominent art panels on the western wall of the western alcove (Table 8). In contrast, the greatest array of preform motifs (hand stencils and

TABLE 5 Interpretation of age ranges of hand stencils (number of stencils per size class: note overlap of potential age classes in bold).

Size class (cm)	Infant	Child	Adolescent	Adult female	Adult male
5.5	**1**	**1**			
6.0					
6.5		**9**	**9**	**9**	
7.0		**8**	**8**	**8**	
7.5		**9**	**9**	**9**	**9**
8.0			**4**	**4**	**4**
8.5			**8**	**7**	**7**
9.0					3
9.5					2
10.0					
10.5					1
11.0					
11.5					

TABLE 6 Possible age ranges for hand prints (number of prints per size class: note overlap of potential age classes in bold).

Size class (cm)	Infant	Child	Adolescent	Adult female	Adult male
5.5					
6.0		**1**	**1**	**1**	
6.5		**2**	**2**	**2**	
7.0					
7.5			**7**	**7**	**7**
8.0					1
8.5					12
9.0					
9.5					1
10.0					
10.5					1
11.0					1
11.5					1

TABLE 7 Distribution of the art technique numbers by art panel across the Buraminya shelter (from west to east).

Art Panel Technique	A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q	R	S	T
Scratchings																		3	
Paintings	11	1	1	1	3	2		6				5		1					2
Drawings	19	29	3	1	1	1		1	3						2	2			
Stencils		16	2				1	17	1	5	10	5	2	9	2	7	4	8	
Prints							2	1		5	18	35							

prints) occurs on both sides of the western alcove, forming an arc across the outer portion of inner ceiling of the alcove (Art Panels H, L–M; Figure 3).

THE ART SEQUENCES

Eighty-five instances of superpositioning were recorded, involving 125 motifs. Combining common colour/technique combinations from each of the individual art panels, the number of sequences can be reduced to 21 (Figure 16). Although no overall sequence of the art is demonstrated from this table, on the basis of the sequences and the relative preservation of the individual motifs involved, a most likely single sequence for the shelter as a whole can be proposed (Figure 17).

As, through its ability to penetrate into the bedrock rather than remain on the surface, sprayed pigment (through stencilling in this case) tends to survive longer than applied pigment (here printing) (cf. Clarke 1978). Hence, hand stencils produced at the same time as hand prints would tend to survive in better condition over time. As the hand prints here are notably better preserved than the hand stencils (Figure 18), it is most likely that they are considerably more recent. This is reinforced by the eight instances where hand prints are superposed over hand stencils (4 red and 4 orange prints

TABLE 8 Motif type numbers by Art Panel. Table division between freeform and preform motif types.

Motif Type	A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q	R	S	T	Total
Bar	1																			**1**
Bar pair		1																		**1**
Bar row	1	1	5	1																**8**
Bird track 3t	2				2	2														**6**
Bird track 4t		1						1												**2**
Bird track trail		1																		**1**
Boomerang																		1		**1**
Design branched	1																			**1**
Design simple		1	1					1	1									2		**6**
Design complex																		1		**1**
Dot				1																**1**
Dot pair												2								**2**
Dot row											1									**1**
Line	7	16	14		2	1		1	2					1		1				**45**
Lines aggregate		4																		**4**
Line curved		1	1																	**2**
Line pair	1		2																	**3**
Line set	1																			**1**
Line undulating															1	1				**2**
Oval barred			1																	**1**
Ovoid	4	1																		**5**
Macropod tracks	1																		1	**2**
Snake															1					**1**
V-shape			1																	**1**
Hand left		4	1					5		2	6	1	2	4	2	1	4	4		**36**
Hand right		6					3	10		4	1	21		2		5				**52**
Hand unclear		4						1	1	1	9	10		3		1		1		**31**
Hand ('Variant V1')			1					2		1		1								**5**
Hand ('Variant V2')											7									**7**
Hand smear												3								**3**
Total	**19**	**41**	**27**	**2**	**4**	**3**	**3**	**21**	**4**	**8**	**24**	**38**	**2**	**10**	**4**	**9**	**4**	**9**	**1**	**233**
Fragments	11	5	9					4		1	4	7						2	1	44

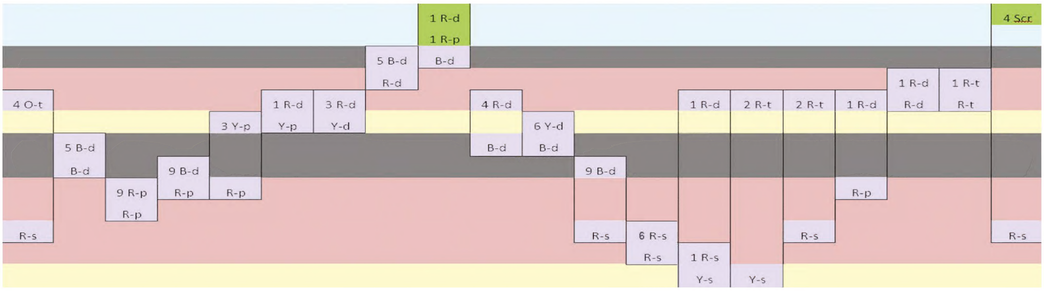

FIGURE 16 Various colour/technique superposition sequences at Buraminya. In each bracketed layer group, the upper motif class overlies the lower and the number of instances in the upper class indicated.

In each cell, motif colour (upper case), precedes the technique (lower case), O = orange, R = red, B = black, Y = yellow (also represented by the coloured bands, dr = drawing, p = Painting, t = print, s = Spray (stencil), Scr = Unpatinated scratching, green rectangles represent the most recent motifs at the site.

over red stencils). As there is a similarity of pigment preservation of the prints across the shelter suggests the red prints were produced at one time and the orange prints at a later date, and that all of the prints post-date the stencils.

The distribution of the art techniques throughout the shelter also suggests a change in focus of art production through time in addition to a change of motif types:

- initially hand stencils were placed throughout the shelter but focused around the inner area of the western end (the most sheltered area); and
- subsequently the focus shifted to the previously unused panels on the western wall and the higher area of the central ceiling.

This dichotomy suggests there was a general trend among the later artists of respecting the existing art of the earlier time. While there is a group of hand stencils on the left side of Art Panel B, the absence of hand stencils to the right and on the adjacent Art Panel A may be attributed to the deterioration of the earlier wall surface in this more exposed art panel. The overall poor preservation of the hand and boomerang stencils compared with that of the other motifs suggests a considerable time passed between the two art phases.

The division of the red paintings from the red stencils that separate the art phases is based on the differential preservation of their respective pigments, with the red paintings notably better preserved.

AGE OF THE ART

No firm dates have been established for the art at Buraminya or any other art from the south-west of Western Australia (Mitchell 2016; Rossi 2014, 2020). The initial occupation of the South-west has been shown to be greater than 45 ka (Allen and O'Connell 2014). From Rossi's excavation at Mulka's Cave (near Hyden, 300 km to the west, but within a similar granite dome and also with a high number of hand stencils) she concluded that the cave and the nearby camping area were being visited from 8 ka and 6 ka respectively (Rossi 2014: 45). If there was a greater range of resources in the Hyden area compared with around Buraminya, it is possible that these dates may precede the use of Buraminya, but a mid-Holocene date cannot be dismissed at this stage. Art production at Buraminya appears to have largely ceased prior to 1896, as graffiti from that time overlies the art (O. Dymer 1896).

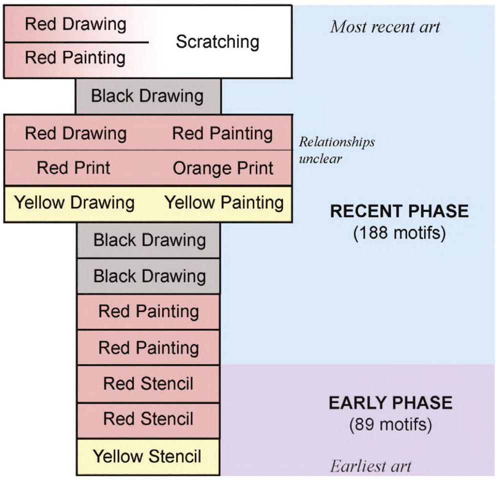

FIGURE 17 Colour/technique sequence within the two-phase art sequence for the Buraminya art site.

DISCUSSION

The rock art at Buraminya is the most decorated rock

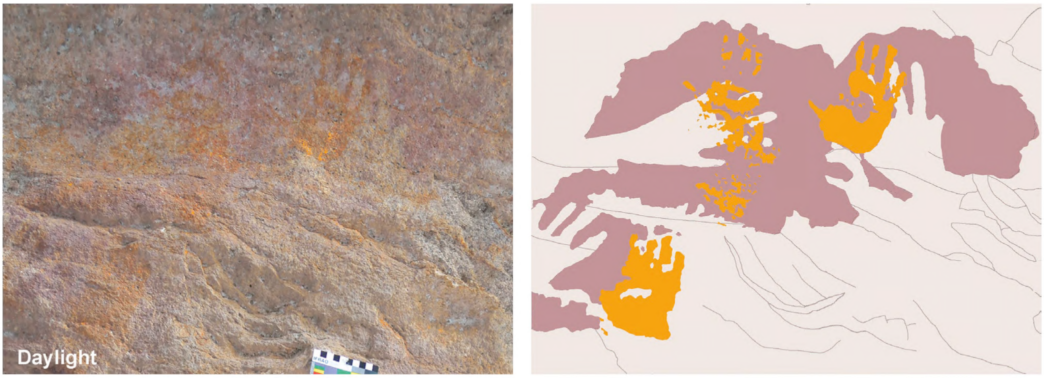

FIGURE 18 Photograph and photo-tracing showing the difference in preservation of the orange hand prints superposed over red hand stencils.

art site in the Ngadju Native Title area with 277 motifs presented in five different techniques. The art consists of both preform and freeform motifs in similar numbers with red being the most dominant colour in both forms. The art comprises two periods; and early phase of stencils (primarily hand stencils of adult men, but children and adolescent and/or adult women are also present). The later and most recent phase includes the freeform motifs (paintings, drawings and scratchings) and hand prints. As with the earlier phase, a range of hand print sizes occur suggesting that the shelter throughout its periods of use was visited by family groups. This does not discount the utilisation of the shelter by discrete social groups at particular times or a change in site status over time, as has been documented elsewhere (e.g. Gunn et al. 1997).

The art of the second art site at Cave Hill consists of 40 red hand prints, 9 red hand stencils, one white hand stencil, and nine red fragments. As at Buraminya, the prints are superposed over the stencils and the age range of the hands ranged from children to adult males.

Although yet to be compared in detail, the motifs reflect the repertoire of both the Noongar rock art tradition to the west and south (Gunn et al. 2017) and the less studied Desert Art to the north-east (Mountford 1939, 1965; Tindale 1959). The connection to Noongar art is in the common motifs of long lines along with hand stencils and hand prints, while that to the Desert Art is through the use of long lines, branched designs, macropod and bird tracks and track trails. There are, however, notable differences to both areas (such as the paucity of white pigment) and suggest that Buraminya is in an area between two major art/cultural areas and had affiliations with both groups.

Also, the notable art sites of Buraminya, the Ballardong Noongar Mulka's Cave, 400 km to the west (2006b) and the Tjaltjraak (Eastern) Noongar site of Marbaleerup, 100 km to the south (Gunn et al. 2017), are all locally outstanding art sites and have common repertoires with each other. This suggest that, while not aggregation sites as defined by Conkey (1908), the three places may be at least local trade and ceremonial sites involving adjacent peoples from these three language groups.

While the date of first art at the site is unknown, but probably mid to late Holocene, the cessation of art appears to just prior to 1896 (given the fresh appearance of some of the drawn pigments and the date of the overlying graffiti). This time was soon after the development of Hunt's Track in the 1860's and the spread of prospectors throughout the countryside with the first discovery of gold at Coolgardie in 1892, Kalgoorlie in 1893 and Norseman in 1894 (Eastern Goldfields Historical Society 2023). 1896 was also the year the Goldfields Railway opened, thus increasing the number of non-Aboriginal people exploring for gold and sandalwood. Such an influx of wide-ranging invaders into Ngadju land and the consequent attraction of Aboriginal people to the developing mining towns may have seen the cessation of art production and a lessening of Ngadju use of the distant Buraminya rock shelter.

CONCLUSION

Buraminya is one of only two rock art sites recorded in Ngadju Country and is of high cultural significance to the Ngadju people today. On the basis its art (high motif numbers, wide variety, and the two-phase art sequence) Buraminya also stands as a major regional rock art site.

This paper has quantified the formal characteristics of the rock art assemblage at Buraminya: an assemblage of 277 individual motifs. These consist of:

- four colours: red (70%), black (21%), yellow (6%), orange (2%) and unpatinated scratching (1%);
- five techniques: stencilling (32%), printing (21%), painting (12%), drawing (33%), scratching (1%); and

- twenty-six motif forms: freeform (85%) and preform (15%).

These results also include two previously undocumented aspects of the art of southern Western Australia were also recorded: the use of scratching as a technique, and the combination of hand stencils and hand prints in a single composition. This quantification now avails this art assemblage to be compared with other assemblages from adjacent regions and beyond.

Buraminya is one of three now recorded sites in south-western Western Australia that have unusually high numbers of hand stencils accompanied by (later) large painted/drawn designs. Each of these three sites occur within a different language area (as of at the time of contact with Europeans) and each have, in addition, unique aspects to their art. The three sites, each over 100km apart, are seen as representing a form of aggregate site, each within their own land but used by the all three groups. These focal sites most likely acted as places of trade and ceremony between these, and possibly other, groups.

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